Decay of Douglas-Fir by Sparassis radicata in Arizona

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ABSTRACT

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Sparassis radicata is one of the major causes of a brown root and butt rot of Douglas-fir in the Santa Catalina Mountains of Arizona. Of 50 recently fallen Douglas-firs with a brown root and butt rot, decay was attributed to *S. radicata* in 30% of the trees, to *Phaeolus schweinitzii* in 62% of the trees, and to both fungus species together in 8% of the trees. Agar-block decay tests showed that both dikaryotic and homokaryotic isolates of *S. radicata* cause a brown cubical decay in Douglas-fir and ponderosa pine wood comparable to that found in naturally decayed roots and butts. Results of genetic analysis of mating-type factors suggest that *S. radicata* spreads from tree to tree through root grafts or root contacts.

Additional key words: root-rotting fungi.

Sparassis radicata Weir was described (17) from northwestern U.S. and British Columbia as the cause of a root rot of several conifer species. It has since been listed in several host-fungus indices (1, 4, 7, 13, 15) but there are no other studies on its importance in decay of North American timber species.

Sparassis radicata is common in coniferous forests of Arizona (4); it has been reported on Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], ponderosa pine (*Pinus ponderosa* Laws.), white fir [*Abies concolor* (Gord. et Glend.) Lindl.], and southwestern white pine (*Pinus strobiformis* Engelm.). Because these tree species are important in timber production, watershed protection, and aesthetics in high-elevation recreational areas in the state, we carried out a study of decay by *S. radicata* in Arizona conifers. Our morphological studies of basidiocarps and cultures of *S. radicata* and related species were reported previously (8).

MATERIALS AND METHODS

Field and laboratory studies of decay.—Roots of living Douglas-firs with attached basidiocarps of *S. radicata* were excavated, exposed, and dissected to determine the extent and nature of the rot. Increment borings were taken from the butt to determine the extent of decay above ground line.

Isolates of *S. radicata* were obtained from the margin of visible decay and incubated at 25 C in darkness on 3.0% malt-extract agar. The identity of these cultures was confirmed by comparison with cultures previously obtained from basidiocarps (8) of *S. radicata*.

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To determine relative decay capabilities of homokaryotic and dikaryotic mycelium, a series of standard agar-block decay tests was made by the method of Gilbertson and Canfield (3). Test blocks, 5 × 2 × 2 cm, were cut from sapwood slabs of Douglas-fir and ponderosa pine. Five standard agar-block decay chambers [8-oz (236-cm^3) French squares] for each dikaryotic and homokaryotic isolate and five noninoculated control chambers were prepared for each of the two types of wood. The chambers were incubated for 24 wk at 25 C in darkness.

Incidence of Sparassis radicata.—The incidence of *S. radicata* and its role in windthrow of Douglas-fir was determined in the Bear Wallow, Mt. Bigelow, Mt. Lemmon, Summerhaven, and Marshall Gulch areas of the Santa Catalina Mountains, Pima County, Arizona. The fungi responsible for brown root and butt rot in fifty fallen Douglas-fir trees was determined. These trees had fallen so recently that decay by secondary organisms was not extensive. Determination of the species responsible for the decay and subsequent failure of each tree was based on the presence of basidiocarps, cultural identification, the presence of rot, mycelial characteristics, and trunk and root breakage pattern.

Analysis of mating-type factors.—*Sparassis radicata* was found to possess clamp connections, to be heterothallic with a bipolar type of mating system, and to possess multiple alleles for incompatibility (8). If a fungus is multi-allelic for incompatibility, the probability is high that basidiocarps in close proximity are from the same dikaryotic mycelium if they share the same mating-type factors. Therefore, an analysis of mating-type factors in 18 basidiocarps collected from trees in four mountain ranges in Arizona was used to identify dikaryons and to test the possibility that *S. radicata* moves from tree to tree through root grafts or root contacts.

Collection data for the isolates used were reported previously (8). The two mating types of isolates KJM-274 and KJM-390 were retrieved from the mating system test (8). The two mating types of the remaining isolates (Table 1) were retrieved as follows. Ten single basidiospore isolates (homokaryons) were obtained from each basidiocarp. Then one homokaryon was arbitrarily designated as representing one mating type and the other nine were mated with it. The second mating type was selected from a compatible mating among these pairings.

To determine if any mating-type factors were shared by these 18 basidiocarps, the 36 homokaryons were mated in all combinations in 60-mm diameter plastic petri dishes nearly filled with 3.0% MEA. After 6-7 wk, the matings

TABLE 1. Mating-type factors found in 18 basidiocarps[a] of *Sparassis radicata* collected from trees in four mountain ranges in Arizona.

Basidiocarp	Isolate no.	Allele	Location	Mountain Range
KJM-274	1	A_1	Bear Wallow	Santa Catalina
	2	A_2		
KJM-391	3	A_2	Mt. Lemmon	Santa Catalina
	4	A_3		
KJM-392	5	A_4	Bear Wallow	Santa Catalina
	6	A_5		
KJM-463B	7	A_6	Treasure Park	Pinaleno
	8	A_7		
JPL-190	9	A_8	Mt. Lemmon	Santa Catalina
	10	A_9		
KJM-468	11	A_{10}	Moonshine Creek	Pinaleno
	12	A_{11}		
KJM-467	13	A_{12}	Hospital Flat	Pinaleno
	14	A_{13}		
KJM-461	15	A_6	Shannon Park	Pinaleno
	16	A_{14}		
KJM-450	17	A_{15}	V. T. Lake	Kaibab Plateau
	18	A_{16}		
JPL-187	19	A_3	Mt. Bigelow	Santa Catalina
	20	A_4		
KJM-463A	21	A_7	Treasure Park	Pinaleno
	22	A_6		
KJM-390	23	A_3	Mt. Bigelow	Santa Catalina
	24	A_4		
KJM-389	25	A_4	Mt. Bigelow	Santa Catalina
	26	A_3		
KJM-469B	27	A_{17}	Moonshine Creek	Pinaleno
	28	A_{16}		
KJM-469D	29	A_{16}	Moonshine Creek	Pinaleno
	30	A_{17}		
KJM-469C	31	A_{17}	Moonshine Creek	Pinaleno
	32	A_{16}		
KJM-469A	33	A_{17}	Moonshine Creek	Pinaleno
	34	A_{16}		
KJM-469E	35	A_{17}	Moonshine Creek	Pinaleno
	36	A_{16}		

[a]All on Douglas-fir except KJM-450 which was on ponderosa pine.

were examined for clamp connections. Positive matings (clamps present) show that no alleles were shared by a particular pairing and negative matings (clamps absent) that an allele was shared. Negative matings were rechecked after an additional 4 wk to confirm that clamps were not present and then were replicated to confirm their incompatibility.

RESULTS

Studies on decay in nature.—Basidiocarps of *S. radicata* under living conifers always were associated with a soft, cheesy, yellowish-brown to brown, carbonizing root rot. Decay developed in both the heartwood and sapwood and had a strong turpentine odor. A dark-purple to black pitchy zone was sometimes found in the region of outer heartwood. Elongated pockets formed in decayed heartwood and were filled with white mycelium. Early decay was a dull reddish-brown and in most cases was difficult to detect.

Decay also was found in the butts of some trees, and in one fallen Douglas-fir it extended up to 4 m above the ground line. Decay in the butts was confined to the heartwood and is very similar to the decay caused by *Phaeolus schweinitzii* (Fr.) Pat. Yellowish to light-brown resinous crusts and thin, scattered patches of white mycelium developed between cubes of advanced decay.

Agar-block decay studies.—Both dikaryotic and homokaryotic isolates of *S. radicata* produced a brown rot in sapwood blocks of ponderosa pine and Douglas-fir. The rot appeared the same for both types of mycelium and was similar to that found in nature associated with basidiocarps.

The relative decay capabilities of homokaryotic and dikaryotic mycelium in agar-block decay tests are shown in Table 2. These data show no apparent differences in the decay capability of the two types of mycelium in either type of wood.

Incidence of Sparassis radicata in the Santa Catalina Mountains.—*Sparassis radicata* and *P. schweinitzii* were the only fungi that caused a brown root and butt rot in the 50 fallen trees examined. Roots of one tree also contained areas of a white pocket rot caused by *Inonotus* tomentosus (Fr.) Gilbn. Of these fallen trees, the failure of 15 (30%) was attributed to *S. radicata*, 31 (62%) to *P. schweinitzii*, and 4 (8%) to *S. radicata* and *P. schweinitzii* together.

The morphology of the mycelium in the decay and the breakage pattern of the decayed wood were two characters used to differentiate the failure of Douglas-fir caused by *S. radicata* from that caused by *P. schweinitzii*. The mycelium of *S. radicata* is white, and the hyphae have clamp connections and spatulate tips. Mycelium of *P. schweinitzii* is yellowish-white, and the hyphae have no clamp connections. Trees with decay attributed to *S. radicata* were broken at or below ground line and had parts of their root systems exposed. Those decayed by *P. schweinitzii* were broken from 0.3-4 m above ground line and had no exposed roots. The four trees with both fungi present had a breakage pattern like that caused by *S. radicata* alone. The results of the incidence study and the correlation of *S. radicata* and *P. schweinitzii* to the breakage pattern on Douglas-fir are summarized in Table 3.

Mating-type factor analysis.—A duplication of mating-type factors occurred in several dikaryotic isolates (Fig. 1). Seventeen alleles for incompatibility were found in the 18 basidiocarps (Table 1). Three isolates (JPL-187, KJM-389, and KJM-390) shared factors designated as A_3 and A_4. Isolates KJM-389 and KJM-390 were from basidiocarps on roots of adjacent living Douglas-fir trees 1 m apart. Isolate JPL-187 was from a basidiocarp on the roots of a Douglas-fir stump 10 m from the two living trees.

The only other isolates that shared the same two mating-type factors came from basidiocarps that were collected on the same root or roots of the same tree. Isolates KJM-463A and KJM-463B came from basidiocarps on the same root of a living Douglas-fir and shared the factors A_6 and A_7. Isolates KJM-469A, KJM-469B, KJM-469C, KJM-469D, and KJM-469E came from basidiocarps collected around a single living Douglas-fir, and shared factors A_{16} and A_{17}. Another basidiocarp (KJM-468) was collected approximately 50 m from the KJM-469 series and did not share any of their mating-type factors.

Two other basidiocarps (KJM-391 and JPL-191)

TABLE 2. Weight-loss of Douglas-fir and ponderosa pine wood blocks decayed for 24 wk by *Sparassis radicata*

Isolate	Douglas-fir: Range of weight loss[b] (%)	Douglas-fir: Weight loss[c] (%)	Ponderosa pine: Range of weight loss (%)	Ponderosa pine: Weight loss (%)
RLG-8243	10.5 - 19.5	15.8	9.7 - 14.9	12.6
KJM-274	13.7 - 18.9	17.2	17.1 - 18.3	17.4
KJM-279	8.8 - 24.9	16.9	10.3 - 19.6	15.2
JJH-1	11.9 - 15.6	13.5	13.5 - 18.8	15.1
KJM-274 A_1[a]	14.6 - 21.2	19.8	13.5 - 15.5	14.5
KJM-274 A_2	15.8 - 17.8	17.1	17.4 - 22.8	19.4
Control	0.5 - 1.0	0.6	0.4 - 1.1	0.7

[a]Homokaryons KJM-274 A_1 and KJM-274 A_2 represent the two mating types obtained from dikaryon KJM-274.
[b]Lowest and highest % weight loss determined for five test blocks exposed to each isolate, based on initial oven-dry weight.
[c]Percentage weight loss determined for five test blocks exposed to each isolate, based on total initial oven-dry weight and total weight loss.

collected from living Douglas-firs 25 m apart did not share any mating-type factors. The balance of the isolates were from widely separated trees and none shared the same two mating-type factors.

DISCUSSION

Sparassis radicata decays members of the Pinaceae only and Douglas-fir is the main host. It has not been found below 2,440 m elevation in Arizona.

Weir (17) reported that in the Pacific Northwest, the decay produced by *S. radicata* is confined to the roots and is found in both the heartwood and sapwood. We concur that *S. radicata* decays both the heartwood and sapwood of the roots. However, in the upper portions of the roots near the butt of the tree, the heartwood is often decayed while the sapwood is still sound. *Sparassis radicata* rot commonly extended into the butt in the Douglas-fir trees we examined. Butt decay was confined to the heartwood.

Weir (17) also concluded that the fungus is parasitic on the roots of conifers and invades the heartwood after living tissues of the root have been killed. Although we concluded that *S. radicata* weakens the root system of trees and subsequently causes their failure, we did not find any standing trees that could be identified as having been killed by the fungus.

It is not known how *S. radicata* invades living trees. Our observations indicate that fire scars or other aboveground wounds are not important as infection courts. Douglas-fir has thick bark and is highly resistant to fire damage. No visible fire scars or any evidence of callosed-over scars or wounds were present on the living Douglas-firs on which basidiocarps of *S. radicata* were found. Southwestern white pine has thin bark and is extremely susceptible to fire damage. *Sparassis radicata* was found on southwestern white pine only once and no fire scars or other wounds were evident on the tree. Weir (17) stated that "mycelium attacks the bast of the roots and later the wood producing a yellow or brown carbonizing rot". This indicates direct penetration of roots by the fungus, but proof is lacking.

We suggest that *S. radicata* spreads from tree to tree through root grafts or root contacts as do such major root-rotting fungi of conifers as *Phellinus weirii* (16), *Inonotus tomentosus* (18), and *Fomitopsis annosa* (2,5). This suggestion is based on analysis of mating-type factors. We recovered three isolates with two shared mating-type factors from basidiocarps on two trees separated by 1 m and a stump separated from these trees by 10 m. Therefore, we conclude that they were from the same dikaryotic mycelium. The proximity of the trees and the stump was such that root grafts or root contacts could have occurred. We concluded that the dikaryotic mycelium either grew through connected roots of the trees and the stump, or that it moved through the soil, either directly or by surviving on humus or buried wood, before attacking the roots. We ruled out the latter because there is no evidence that the fungus produces rhizomorphs or other structures capable of surviving and growing directly in soil. In addition, in an area with many basiodiocarps producing large numbers of basidiospores carrying many different mating-type factors, it seems unlikely that a single dikaryon would become established, spread in the soil, and infect several adjacent trees to the exclusion of other dikaryons. Therefore, we consider it most probable that all three of the isolates came from the same dikaryotic mycelium that grew through connected roots of the trees and the stump. Additional evidence for our conclusion is that the only other isolates that shared the same two mating-type factors, came from basidiocarps in the same root or roots of the same tree. Isolates from basidiocarps collected in the same vicinity but 25 m and 50 m apart did not share the same two mating-type factors. McMinn's work (9) indicates that Douglas-fir roots ordinarily do not extend these distances, therefore root grafts or contacts probably did not occur between trees separated by 25 m or 50 m.

Mycelium of *S. radicata* surviving in roots on stumps and dead trees could provide an important source of inoculum for surrounding healthy trees as well as for the next rotation of trees when healthy roots come in contact with infected ones.

TABLE 3. Incidence of *Sparassis radicata* and *Polyporus schweinitzii* correlated with breakage type on Douglas-fir in the Santa Catalina Mountains in Arizona

Location	No. of trees examined	Failure attributed to *S. radicata*		Failure attributed to *P. schweinitzii*		Failure attributed to both *S. radicata* and *P. schweinitzii*	
		No. with breakage type A[y]	No. with breakage type B[z]	No. with breakage type A	No. with breakage type B	No. with breakage type A	No. with breakage type B
Mt. Bigelow	8	0	2	6	0	0	0
Bear Wallow	9	0	3	4	0	0	2
Marshall Gulch	9	0	5	4	0	0	0
Summerhaven	7	0	1	6	0	0	0
Mt. Lemmon	17	0	4	11	0	0	2
Totals	50	0	15	31	0	0	4

[y]Based on presence of basidiocarps, mycelium isolated and/or decay and mycelial characteristics.

[z]A = trees broken 0.3-4 m above ground line with no roots exposed. B = trees broken at or below ground line with part of root system exposed.

None of the studies (2, 5, 16, 18) in which *P. weirii*, *I. tomentosus*, and *F. annosa* were shown to move through root grafts or root contacts was done by genetic analysis of the mycelium. This analysis can be carried out readily only on species that are heterothallic and form clamp connections. These other root-rotting fungi, along with *Armillaria mellea* (11), do not have a dikaryotic mycelial stage with clamp connections and their mating systems are unknown.

Agar-block decay tests show that in 24 wk there is no apparent difference in the decay capability of homokaryotic and dikaryotic mycelium of *S. radicata*. Therefore, it is possible that homokaryotic mycelium could cause decay in living trees. However, we did not isolate any homokaryons from trees with decay attributed to *S. radicata*.

Martin and Gilbertson (8) have shown from basidiocarp and cultural studies that European and Japanese isolates and specimens of *Sparassis crispa* Wulf. ex Fr. are conspecific with *S. radicata*. Our studies of *S. radicata* and those of *S. crispa* by Pawsey (10), Schonar (12), and Siepmann (14) in Europe and by Kamei and Igarashi (6) in Japan also show other similarities. Decay caused by *S. crispa* is similar to that caused by *S. radicata*. Pawsey (10) reported that in Sitka spruce plantations in Great Britain, the incidence of butt rot caused by *S. crispa* is less than that caused by *P. schweinitzii* and that both fungi may occur in the same tree. However, Schonar (12) reported that the incidence of *S. crispa* was greater than *P. schweinitzii* in Scots pine in Baden-Württemberg,

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
1			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
2			−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
3	+	−			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
4	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	−	+	+	−	+	+	+	+	+	+	+	+	+	+
5	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	−	−	+	+	+	+	+	+	+	+	+	+	+
6	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
7	+	+	+	+	+	+			+	+	+	+	+	+	−	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+
8	+	+	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
9	+	+	+	+	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
10	+	+	+	+	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
11	+	+	+	+	+	+	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
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13	+	+	+	+	+	+	+	+	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
14	+	+	+	+	+	+	+	+	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
15	+	+	+	+	+	+	−	+	+	+	+	+	+	+			+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+
16	+	+	+	+	+	+	+	+	+	+	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
17	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
18	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			+	+	+	+	+	+	+	+	+	−	−	+	+	−	+	−	+	−
19	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+			+	+	−	+	+	−	+	+	+	+	+	+	+	+	+	+
20	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+			+	+	+	−	−	+	+	+	+	+	+	+	+	+	+	+
21	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+
22	+	+	+	+	+	+	−	+	+	+	+	+	+	+	−	+	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+
23	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+			+	−	+	+	+	+	+	+	+	+	+	+
24	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+			−	+	+	+	+	+	+	+	+	+	+	+
25	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	−			+	+	+	+	+	+	+	+	+	+
26	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	−	+			+	+	+	+	+	+	+	+	+	+
27	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			+	−	−	+	−	+	−	+
28	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+			−	+	+	−	+	−	+	−
29	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	−			+	−	+	−	+	−
30	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+			−	+	−	+	−	+
31	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	−			−	+	−	+
32	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	+			+	−	+	−
33	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	−	−	+			−	+
34	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	+	+	−			+	−
35	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	−	−	+	−	+		
36	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	+	+	−	+	−		

Fig. 1. Results of pairing 36 homokaryotic isolates representing the two mating types from each of 18 basidiocarps of *Sparassis radicata* collected from trees in four mountain ranges in Arizona.

Germany. *Sparassis crispa* was isolated from 27.2% of the decayed trees he studied compared to 16.2% for *P. schweinitzii*. Siepmann (14) found *P. schweinitzii* and *S. crispa* to be the main causes of decay in a 55-yr-old stand of Douglas-fir in Germany. He considered it likely that both fungi grew into the Douglas-fir roots from dead roots of pine from the previous crop on the site.

It is possible that *S. radicata* is important in other Douglas-fir regions of western North America, but owing to the similarity of its decay to that caused by *P. schweinitzii*, it may have been overlooked.

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