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Relative Fusiform Rust Resistance of Loblolly and Slash Pine Sources and Families in Georgia and South Carolina

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Abstract

Loblolly and slash pine seedlings from the fusiform rust resistant orchards developed cooperatively by the USDA Forest Service and the Georgia Forestry Commission had significantly less rust 7 to 8 years after planting on four of five sites in the Southeastern United States than seedlings of the same species from orchard sources developed primarily for silvicultural improvement. Loblolly and slash pine family plantings varied in rust susceptibility on eight sites after 5 to 7 years. Although rust incidence was relatively low, many families contributed to a significant interaction effect of family by location in the 7-year-old planting. This significant interaction indicates that relative performance of families is affected by the variation in virulence of the rust pathogen at different locations. This finding supports the hypothesis that mixes of resistant families will limit fusiform rust infections more effectively than single family plantings.

Keywords: Concentrated basidiospore spray, disease resistance, rust fungus, rust susceptibility.

Introduction

The study of relative fusiform rust resistance in pine families and sources in field plots is the final indicator that the trait is valuable. Greenhouse inoculations with the concentrated basidiospore spray (CBS) system (Matthews and Rowan 1972) or the forced air system (Snow and Kais 1972) are useful techniques in rust resistance screening. These provide information about the relative rust resistance of families or sources compared to other families or sources exposed to a limited inoculum source of the fungus under uniform conditions. However, the greenhouse results should be compared to field tests because the pathogenicity of the rust fungus can vary considerably from location to location. Furthermore, very young seedlings inoculated in the greenhouse may not respond to the rust fungus in the same manner as trees growing in the field.

Previously, Miller and Powers (1983) demonstrated that rust incidence in field plantings in central Georgia and in CBS inoculations correlated well for several loblolly pine families. Similarly, Powers and Kuhlman (1987) reported that results from the CBS inoculations generally correlated well with field progeny tests in Greene County, Georgia (GA). Recently, Hodge and others (1993) reported that each mix of six resistant slash or resistant loblolly pine families always had less rust than mixes of six susceptible slash or susceptible loblolly pine families in six plantings in Georgia, Florida, and Mississippi. Sluder (1988) has shown that some loblolly pines selected for resistance in field plantings can dramatically reduce rust incidence in high hazard areas.

The virulence of the rust fungus can vary with location. Virulence is the genetic capacity of some isolates of the fungus to overcome resistance in some pine families. Powers and others (1977) and Snow and others (1975) reported how various loblolly and slash pine families responded differently to rust inocula from different geographic locations. Both reported that some rust isolates caused more disease on some families than on other families. Griggs and Walkinshaw (1982) reported that a single-gall aeciospore isolate was virulent on two slash pine families and caused galls on nearly 100 percent of the seedlings, while another single-gall isolate was completely avirulent on these families and produced no galls. Kuhlman (1990) showed that single-gall aeciospore isolates with virulence toward specific resistant families were present in some populations, but the frequency of occurrence was often low. However, a resistant slash pine family was more susceptible to rust isolates from infected family members than to isolates from a wild population (Snow and others 1976).

Many studies report that host genotype x environment (location) interaction for fusiform rust infection is of little importance in either slash or loblolly pine. This suggests that any variations in the virulence of the rust fungus have not affected the incidence of infection. Kinloch and Stonecypher (1969) found no significant environmental effect on relative ranking of rust susceptibility among control- and open-pollinated loblolly pine families planted on sites with various cultural histories within a 4-kilometer area in south Georgia. Wells and others (1982) reported that six loblolly sources from west of the Mississippi River had stable resistance, whereas resistant sources from east of the river were generally less stable at three sites in Louisiana, Mississippi, and Alabama. Hodge and others (1993) reported the ratios of infection in mixes of resistant and susceptible seedlots of slash and loblolly pines were stable on six sites in Georgia, Florida, and Mississippi. However, in a geographic seed source study, Wells and Wakeley (1966) report the seed source x location interaction effect on rust resistance was highly significant in their series that included sources and planting sites from Maryland to Texas. This interaction was distributed randomly over the study area and was not due to a few seed sources or a single site. No interaction occurred in the less widely distributed series that did not include seed sources or planting sites in Maryland or Texas.

The primary objective of the studies reported in this paper was to determine if orchard and family sources resistant to fusiform rust in greenhouse tests would be resistant in field plantings in Georgia and South Carolina. A secondary objective was to determine if rust infection varied on different sites in the Southeastern United States because virulent isolates of the rust fungus were present. Fourteen different studies were established between 1986 and 1989. Six orchard source plantings compared rust resistant seedlings from the Georgia Forestry Commission (GFC)/USDA Forest Service (USFS) rust resistant orchards of slash and loblolly pines with commercially available pines of these two species selected primarily for silvicultural improvement by the GFC. Eight family plantings compared individual families of loblolly and slash pines. All plantings occurred in areas rated as high hazard in region-wide surveys (Phelps 1974, Bechtold and others 1992).

Methods

Source Studies

Fusiform rust resistant slash and loblolly pine seeds were collected in the GFC/USFS rust resistant orchards and improved slash and loblolly pine seeds were collected in the GFC silviculturally improved orchards. Seedlings were approximately 9 months old when lifted from the nursery beds.

In the 1986 study, seedlings were machine-planted on the Savannah River Site (forests managed by the USFS for the Department of Energy) in Barnwell County, South Carolina (SC). The three replications of each seed source had eight rows of seedlings. Within replications, seed sources were randomly assigned to each location. The length of the rows varied from 160 to 275 meters (m). Seedlings were spaced at 2.5-m intervals within the rows, and rows were 3 m apart. In 1994, within each source replication, the presence of branch or stem galls for all trees in two rows and the diameter at breast height (d.b.h.) of every second tree in one row were recorded. Total trees examined for each source varied from 469 to 511 trees.

In 1987, seedlings were hand-planted on the Savannah River Site in Aiken County, SC; on private lands in Mitchell and Sumter Counties, GA; and on GFC land in Baldwin County, GA. The two sites on private land had been previously used for agricultural crops. The other two sites had been previously forested. The four replications of each seed source had eight rows of seedlings with 15 seedlings per row (120 seedlings per replication). Sources were randomly assigned to locations within replications. Seedlings were spaced at 2.5-m intervals within rows, and rows were spaced at 3 m.

In 1989, a planting was made in Barnwell County, SC. Each source was spaced in four rows with 25 seedlings per row. Between January and March 1994, rust incidence (stem galls, branch galls, or rust-associated mortality (RAM)), survival, and growth measurements were made in all plots. Growth was determined as total tree height to 0.1 m or d.b.h. to the nearest 0.1 centimeters.

Family Plantings

In 1987, loblolly and slash pine families were planted in areas adjacent to the source studies in Barnwell County, SC; Mitchell County, GA; Sumter County, GA; and Baldwin County, GA. At each site, 7 to 10 half-sib loblolly pine families and 6 to 7 half-sib slash pine families were hand-planted in 1 to 9 replications with 20 seedlings per replication per family. All except 1 of 9 slash families and all 11 loblolly families were planted at 2 to 4 locations to determine variations in rust incidence among locations.

In 1988, half-sib slash and loblolly pine families were hand-planted on industry lands in Colleton County, SC; Effingham County, GA; and on the Savannah River Site in Barnwell County, SC. Previously, the three sites had been forested. At each site, 10 to 13 loblolly families and 4 to 8 slash families were planted. Twelve of 15 loblolly families and 5 of 9 slash families were planted at more than 1 location. Twenty seedlings per replication per family and 1 to 9 replications per family were installed.

In 1989, 19 half-sib loblolly pine families were hand-planted on the Savannah River Site in Barnwell County, SC, on previously forested land. There were 2 to 9 replications per family with 20 seedlings per family per replication.

In 1994, survival, growth, and rust-incidence data were collected. Growth was determined by height to the nearest 0.1 m for the 1989 planting and for the 1988 plantings in Barnwell and Effingham Counties. Growth was determined by d.b.h. for trees in the remaining plantings. The presence or absence of rust galls on all trees were recorded.

Statistical Analysis

The percentage of trees with galls within a replication was calculated for each family, source, or treatment. Both the raw percentages and the arc sines of their square roots were used in the analyses of variance (ANOVA) (SAS Institute 1988). Mean separation was performed with Tukey's Studentized Range (HSD) Test at the 10-percent level of significance.

Results

Source Study

In the 7- and 8-year-old plantations, the rust resistant sources showed significantly better disease resistance than sources selected primarily for silvicultural improvement in four of the five loblolly and three of five slash pine plots (table 1). Interaction among sites for the 7-year-old orchard source plantings was not significant, suggesting these mixes of resistant and improved trees responded similarly on these four sites. Although the largest variation in frequency of trees with galls occurred in the 5-year-old planting, this planting was not replicated and a statistical analysis could not be made. In that planting, rust resistant loblolly and slash pine trees had only 10 percent with galls compared to 44 and 28 percent trees with galls in the improved loblolly and slash sources.

Family Plantings

At best, rust infection levels in these tests were generally moderate, even in the susceptible controls (loblolly 4666-4 and slash MassSus). However, loblolly family 151-491 had 60-percent infection in the 7-year-old study in Barnwell County, SC (table 2), and families 11-10 and 29R had 57 percent and 56 percent infection, respectively, in the 6-year-old planting in Colleton County, SC (table 3). The highest rate of infection (52 percent) of mass susceptible slash pine (MassSus) occurred in the 7-year-old Barnwell County planting. MassSus slash had the highest infection rate among the slash families in five of seven plantings. Family 4666-4 was included in all of the plantings because it has often served as the susceptible standard in CBS greenhouse tests at our lab. In these field studies, this family had an infection rate close to the average for all families at a site. With an average infection of 29 percent in the eight locations, it appears to have field resistance. Notwithstanding, the relatively low average, progeny of 4666-4 had the highest rates of infection in two of eight plantings—the 7-year-old Baldwin County and the 5-year-old Barnwell County (table 4).

Family 153-353 had the lowest gall frequency (4, 5, and 11 percent) for loblolly in each of the three 6-year-old plantings (table 3). Slash family 1663-11 had a low infection rate of 3 to 8 percent on three sites: Barnwell County (6-year-old), Sumter County

Table 1—Frequency of fusiform rust and relative growth of trees from rust resistant and silviculturally improved sources of slash and loblolly pines 7 and 8 years after planting on five sites in Georgia (GA) and South Carolina (SC)

Source	Age					Avg. for 7-yr-olds
	7 yrs	7 yrs	7 yrs	7 yrs	8 yrs	
	Aiken Co., SC	Mitchell Co., GA	Sumter Co., GA	Baldwin Co., GA	Barnwell Co., SC	
- - - - - <i>Trees with galls (percent)</i> - - - - -						
Loblolly						
Resistant	16b ¹	26b	30b	31a	26bc	26b
Improved	24a	43a	46a	41a	40a	40a
Slash						
Resistant	24ab	27b	37ab	32a	17c	30b
Improved	30a	41a	46a	43a	32ab	40a
- - - - - <i>Relative growth (d.b.h., cm)</i> - - - - -						
Loblolly						
Resistant	10.8a	13.3a	12.8a	10.2a	14.0a	12.2a
Improved	10.2a	13.1a	11.8a	10.1a	14.3a	11.9a
Slash						
Resistant	10.6a	12.5bc	11.4a	10.1a	12.3b	11.4a
Improved	10.0a	12.1c	11.1a	10.1a	12.3b	11.1a

¹ For rust incidence and relative growth data, means followed by the same letter within columns are not significantly different at the 10-percent level with Tukey's (HSD) Studentized Range Test.

Table 2—Incidence of fusiform rust galls on 7-year-old loblolly and slash pine families planted on four locations in Georgia (GA) and South Carolina (SC)

Family	MRS ¹	DR ²	Barnwell Co., SC	Mitchell Co., GA	Sumter Co., GA	Baldwin Co., GA
- - - - Trees with galls (percent) - - - - -						
Loblolly						
151-144	11-20	55	35abc ³	20abc	13bcd	32a
151-263	10-5	37	27bc	12bc	17abcd	20abc
151-491	T-601	56	60a	23abc	--	--
151-754	T-605	49	39abc	35ab	36a	29ab
152-61	10-6	74	30bc	18abc	21abcd	--
152-130	T-601	74	26bc	26ab	34ab	--
152-297	11-9	58	41abc	26ab	21abc	--
152-309	29R	57	--	--	16abcd	16abc
153-32	42R	48	41abc	25abc	25abcd	31a
4666-4	4666-4	100	27bc	22abc	31abc	33a
7840-16	7840-16	62	34abc	25abc	25abcd	30ab
Average, loblolly			36	23	24	27
Slash						
1663-11	Dodge 36	68	--	--	8d	3c
2882-23	J18XJ6	39	24bc	14bc	13bcd	24abc
3288-22	Dodge 2	52	25bc	2c	--	--
3297-21	Mitch 10	40	20c	13bc	11cd	4bc
3302-21	Em 5	40	24bc	23abc	17abcd	17abc
3365-8	Dodge 4	59	--	--	17abcd	21abc
4555-4	Ter 2	50	16c	--	--	--
4913-10	Whe 11	77	31abc	20abc	26abcd	--
MassSus	Mix	100	52ab	40a	35ab	26abc
Average, slash			27	19	18	16
Average, loblolly and slash			34	22	22	22

¹ MRS = maternal resistance source (assumed source of resistance).

² DR = disease ratio. It is the frequency of galls on this family compared to those on a susceptible family (in greenhouse test) x 100.

³ Within columns, means followed by the same letter are not significantly different at the 10-percent level with Tukey's (HSD) Studentized Range Test.

Table 3—Incidence of fusiform rust galls on 6-year-old loblolly and slash pine families planted on three locations in Georgia (GA) and South Carolina (SC)

Family	MRS ¹	DR ²	Colleton Co., SC	Effingham Co., GA	Barnwell Co., SC
- - - Trees with galls (percent) - - -					
Loblolly					
151-97	15-42	64	33abc ³	18a	27ab
151-364	10-6	65	--	15a	--
152-387	10-5	03	29bc	4a	6b
153-238	1582-11x	28	29bc	12a	--
153-243	42R	37	--	24a	--
153-353	10R	25	11c	4a	5b
10-5	10-5	49	35abc	24a	33ab
11-10	11-10	45	57a	27a	34ab
11-20	11-20	40	46ab	15a	35ab
29R	29R	59	56a	23a	46a
42R	42R	59	--	26a	36ab
4625-3	4625-3	68	35abc	--	30ab
4666-4	4666-4	100	35abc	27a	28ab
7840-16	7840-16	62	--	21a	--
Average, loblolly			37	19	28
Slash					
10-226	10-226	45	37ab	34a	39ab
1663-11	Dodge 36	68	--	--	6b
2882-23	J18 x J6	39	--	--	37ab
3302-21	Em. 5	40	38ab	19a	23ab
3365-8	Dodge 4	59	--	--	12ab
3384-9	Telf. 37	52	--	30a	28ab
4555-4	Ter. 2	50	29bc	--	--
7703-2	Bull. 6	100	--	17a	38ab
MassSus	Mix	100	41ab	12a	32ab
Average, slash			36	22	27
Average, loblolly and slash			38	22	29

¹ MRS = maternal resistance source (assumed source of resistance).

² DR = disease ratio. It is the frequency of galls on this family compared to those on a susceptible family (in greenhouse test) x 100.

³ Within columns means followed by the same letter are not significantly different at the 10-percent level with Tukey's (HSD) Studentized Range Test.

Table 4— Frequency (percent) of survival and of trees with fusiform rust galls and relative growth (height in meters) of nineteen loblolly pine families in a 5-year-old planting in Barnwell County, South Carolina

Family	MRS ¹	DR ²	Galls	Height (m)	Survival (%)
154-60	3333	15	3c ³	2.45cd	73
152-60	TFS	30	5bc	3.26ab	81
151-791	HH	42	5bc	2.34d	62
151-431	11-9	49	10abc	2.64bcd	58
11-41	--	19	11abc	3.24ab	74
151-307	1495-35	65	12abc	2.82abcd	78
151-91	SML-9	24	12abc	2.77abcd	76
153-517	7-56	30	12abc	3.20ab	58
153-279	29Rx10-5	17	16abc	2.68abcd	70
155-53	11-20MR	53	17abc	2.93abcd	60
152-275	29RxA	45	21abc	3.05abc	83
151-334	T601	44	22abc	3.21ab	73
3906-21	--	77	24abc	2.73abcd	76
151-627	2318	43	25abc	2.81abcd	73
3470-16	--	111	25abc	2.93abcd	79
151-375	15-42	57	26abc	3.04abc	83
3490-15	--	94	26abc	2.78abcd	81
151-445	10-31	57	30ab	3.28a	78
4666-4	--	100	32a	2.79abcd	60
Average			18	2.89	72

¹ MRS = maternal resistance source (assumed source of resistance).

² DR = disease ratio. It is the frequency of galls on this family compared to those on a susceptible family (in greenhouse test) x 100.

³ Within columns means followed by the same letter are not significantly different at the 10-percent level with Tukey's (HSD) Studentized Range Test.

(7-year-old), and Baldwin County (7-year-old) (tables 2 and 3). Slash family 3365-8 had less than half the rate of infection of the mass susceptible control in two of these three plantings. In the 5-year-old loblolly planting, families 154-60, 152-60, and 151-791 had ≤ 5 percent infection, compared to 32 percent infection in family 4666-4 (table 4).

Some families had significant interaction in the ANOVA between rust incidence and location for the 7-year-old, but not for the 6-year-old family plantings. For example, family 151-144 was very resistant in Sumter County (13 percent) but relatively susceptible in Barnwell and Baldwin Counties (table 2). Slash family 2882-23 was quite resistant in Mitchell and Sumter Counties but more susceptible in Barnwell and Baldwin Counties. Slash family 3297-21 was most resistant in Baldwin County.

Survival

Survival in the source and family plantings was generally good with up to 93 percent of the trees still alive and very little rust-associated mortality 6 and 7 years after planting. Loblolly families in Colleton and Mitchell Counties averaged 86 and 85 percent survival, respectively. Slash families also had the best survival in these two locations. The 6-year-old slash family plantings in Effingham County had the poorest survival averaging 41 percent, probably due to a poor site and drought conditions soon after planting.

Growth

In the source plantings, no significant differences in growth occurred between the rust resistant sources and the improved sources (table 1). In the Mitchell County and the 8-year-old Barnwell County plantings, the two loblolly sources had larger diameters than the two slash sources.

In the family plantings, significant differences in growth occurred among families at all locations (tables 4, 5, 6). The stringent Tukey's Studentized Range Test at the 10-percent level used for statistical comparisons indicated a lot of overlap in growth among the families. Slash families generally grew less well than loblolly families. The MassSus slash family had the poorest growth at most locations. Regressions of family growth versus family resistance (gall frequency) were computed, but no significant

relationship between rust incidence and growth was present. Similar comparisons across all locations for the 7-year-old plantings indicated that selecting for rust resistance does not significantly affect growth.

Discussion

On most sites in Georgia and South Carolina, fusiform rust resistant orchard sources of loblolly and slash pines had less rust after 7 to 8 years than orchard sources selected primarily for silvicultural improvement. Because rust resistant orchards are continuously rogued of the most rust-susceptible individuals, seedlings from these orchards should continue to improve in relative fusiform rust resistance.

The interaction of rust incidence among families on different sites indicates that the rust varies in virulence on different sites. Virulence in the pathogen is genetically controlled, just like resistance in the pine host. The presence of interaction indicates that different genes for virulence in the rust population are present on different sites in Georgia and South Carolina. Because predicting the virulence of local rust populations to different rust resistant families is not presently possible, planting a mix of families to ensure a heterogenous rust resistant pine population appears to be the safest means of limiting rust-related losses.

Concern about selecting for rust resistance has been expressed. Some believe growth would suffer, while others feel susceptible trees grow faster and make up any loss to rust. Our data does not support these ideas because no relationship between rust susceptibility and growth was observed. Moreover, in developing these rust resistant families for the USFS/GFC Rust Resistance Orchards, Powers and Kraus (1983) selected in progeny test blocks first for growth and then within the fastest growers selected for rust resistance. The fusiform rust resistant sources grew as well as the silviculturally improved sources, indicating that selecting for rust resistance did not result in growth loss.

Table 5—Growth of loblolly and slash pine families in 7-year-old plantings on four locations in Georgia (GA) and South Carolina (SC)

Family	Barnwell Co., SC	Mitchell Co., SC	Sumter Co., GA	Baldwin Co., GA
- - - - - d.b.h. (cm) - - - - -				
Loblolly				
151-144	10.0bc ¹	13.8bcde	13.8bcd	10.6abc
151-263	9.8bc	14.0bcd	13.9abcd	10.7abc
151-491	12.3a	14.5abc	--	--
151-754	11.1ab	14.8ab	14.8ab	11.3a
152-61	10.5ab	13.3bcdef	14.1abc	--
152-130	9.6bc	15.7a	15.5a	--
152-297	10.1abc	14.1bcd	13.4bcdef	--
152-309	--	--	13.4bcde	10.6abc
153-32	10.0bc	12.9defg	13.4bcde	9.5abcd
4666-4	9.9bc	12.5defg	12.9cdef	10.3abc
7840-16	10.5ab	14.0bcd	13.2bcdef	11.0ab
Average, loblolly	10.4	14.0	13.9	10.6
Slash				
1663-11	--	--	12.5cdef	9.0cd
2882-23	8.9bc	12.1gh	12.0ef	10.4abc
3288-22	9.7bc	10.9h	--	--
3297-21	9.3bc	12.9defg	12.7def	7.8d
3302-21	9.7bc	13.0cdefg	12.4def	9.1bcd
3365-8	--	--	12.6def	9.4abcd
4555-4	9.2bc	--	--	--
4913-10	9.3bc	12.3efgh	12.1ef	--
MassSus	9.0bc	11.6gh	11.8f	9.5abcd
Average, slash	9.3	12.1	12.3	9.2
Average, loblolly and slash	10.0	13.3	13.3	10.1

¹Within columns means followed by the same letter are not significantly different at the 10-percent level with Tukey's (HSD) Studentized Range Test.

Table 6—Relative growth of loblolly and slash pine families in 6-year-old plantings in three locations in Georgia (GA) and South Carolina (SC)

Family	Colleton Co., SC	Effingham Co., GA	Barnwell Co., GA
	<i>dbh (cm)</i>	<i>Height (m)</i>	
Loblolly			
151-97	9.5de ¹	2.55de	4.77abcd
151-364	--	2.76abcde	--
152-387	10.6cd	2.89abcde	4.95abc
153-238	12.0ab	2.99abcde	--
153-243	--	3.07abcde	--
153-353	9.0e	2.62cde	4.16cdef
10-5	12.5a	3.35a	5.71a
11-10	11.7abc	3.39a	5.45ab
11-20	12.3ab	3.41a	5.63a
29R	9.6de	2.63bcde	4.62bcdef
42R	--	3.10abcde	4.47cdef
4625-3	12.0ab	--	4.95abc
4666-4	10.0de	2.61cde	4.42cdef
7840-16	--	2.73abcde	--
Average, loblolly	10.9	2.93	4.91
Slash			
10-226	9.7de	3.41a	4.64bcde
1663-11	--	--	3.98def
2882-23	--	--	4.78abcde
3302-21	11.3bc	3.28abc	4.12cdef
3365-8	--	--	4.07cdef
3384-9	--	3.33ab	4.47cdef
4555-4	11.2bc	--	--
7703-2	--	3.00abcde	3.91def
MassSus	9.2e	3.24abcd	4.60bcdef
Average, slash	10.4	3.25	4.32
Average, loblolly and slash	10.7	3.02	4.49

¹ Within columns means followed by the same letter are not significantly different at the 10-percent level with Tukey's (HSD) Studentized Range Test.

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Loblolly and slash pine seedlings from the fusiform rust resistant orchards developed cooperatively by the USDA Forest Service and the Georgia Forestry Commission had significantly less rust 7 to 8 years after planting on four of five sites in the Southeastern United States than seedlings of the same species from orchard sources developed primarily for silvicultural improvement. Loblolly and slash pine family plantings varied in rust susceptibility on eight sites after 5 to 7 years. Although rust incidence was relatively low, many families contributed to a significant interaction effect of family by location in the 7-year-old planting. This significant interaction indicates that relative performance of families is affected by the variation in virulence of the rust pathogen at different locations. This finding supports the hypothesis that mixes of resistant families will limit fusiform rust infections more effectively than single family plantings.

Keywords: Concentrated basidiospore spray, disease resistance, rust fungus, rust susceptibility.

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