Note Added in Proof Compounds 1 and 2 exhibit the same electrophoretic and thin-layer chromatographic behaviors as *Protogonyaulax* toxins C1 and C2, both of which were cordially provided to us in crystalline forms by Dr. S. Hall, Woods Hole Oceanographic Institution, Woods Hole, MA.

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Germination Responses of Several Species of Rust Spores to 5-Methyl-2-hexanone, Isomers of Ionone, and Other Structurally Related Flavor Compounds

Richard C. French

Uredospores of *Puccinia punctiformis*, *Puccinia chondrillina*, *Puccinia iridis*, and *Uromyces trifolii-repentis* were tested for germination responses to β-ionone, α-ionone, 5-methyl-2-hexanone, and other related compounds. Maximum germination by any treatment ranged from 80 to 90% for the four species. Germination of uredospores of *P. punctiformis* and *P. chondrillina* was stimulated most by 5-methyl-2-hexanone and 2-heptanone. *P. iridis* was stimulated most by β-ionone. *P. punctiformis* was stimulated by α-ionone but not by β-ionone. *P. chondrillina* and *P. iridis* were stimulated by β-ionone but not α-ionone. Both *P. punctiformis* and *P. chondrillina* could be chemically stimulated over a temperature range of 10–25 °C. Uredospores of *U. trifolii-repentis* were stimulated most effectively by β-ionone, followed by α-ionone and octyl cyanide. 5-Methyl-2-hexanone is the third compound (after nonanol and β-ionone) found to be the most effective chemical germination stimulator for certain groups of rust species.

Differences in response of uredospores of various species of rusts to certain flavor chemicals have been reported previously (French and Gallimore, 1971; French et al., 1975a,b, 1977; French and Wilson, 1981). Some of the chemicals studied also have been found in uredospores of several species (French and Weintraub, 1957; Rines et al., 1974). For example, nonanal and 6-methyl-5-hepten-2-one have been identified in rusts, and they also occur naturally as components of flavors and fragrances in a variety of natural products, including citrus peel oils, and other food items (Furia and Bellanca, 1975). These two compounds also have been identified as insect pheromones (Blum, 1969). β-Ionone and 6-methyl-5-hepten-2-one have been found in volatiles from algal cultures, and β-ionone has been reported to inhibit growth of several algal species (Jüttner, 1979). Virtually all of the compounds used in this research have been reported to occur in various natural products. This study of the effect of chemical structure on stimulator activity was conducted to determine the most efficient compound for stimulating spores of several rust species, including two which are pathogens of weeds. This information may be useful in providing effective tools to solve practical problems in uredospore germination, such as obtaining maximum germination in uredospores applied to weed pests in biocontrol operations or causing germination of pathogenic spores at an opportune time for disease control. Determining the structural requirements for chemical stimulation also should provide a starting point for research on mechanism of action.

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MATERIALS AND METHODS

Since rust fungi are obligate parasites, uredospores were produced on the appropriate hosts, usually in the greenhouse. Uredospores or aeciospores of *Puccinia punctiformis* (Strauss) Roehl. were collected in the field from plants of Canada thistle, *Cirsium arvense* (L.) Scop.

Uredospores of *Puccinia chondrillina* Bubak & Syd. were grown on *Chondrilla juncea* L., *Puccinia iridis* (DC) Wallr. on *Iris siberica* L. var. *sanguinea* Ker–Gawl, cv. not known, and *Uromyces trifolii-repentis* Liro var. *fallens* (Arth.) Cumm. on red clover, *Trifolium pratense* L.

Germination experiments were carried out in Conway diffusion cells, which served as individual isolation chambers, as previously described (French et al., 1977). Chemicals were measured and dispensed from Hamilton syringes (1.0 μL) to 2.0 mL of distilled water in the center of Conway cells to give final concentrations of 10–1000 μL/L. For reduction of the quantity of uredospores required for self-inhibition to levels close to zero percent germination, an aliquot (0.5 mL) of each concentration of test chemical was transferred to glass microdishes (24-mm diameter), which also were placed in the centers of the Conway cells. About 1.5 ± 0.2 mg of spores was placed on the test solution in the microdishes. Uredospores were dispersed uniformly with an inoculating loop. This quantity of spores was great enough to reduce germination to a minimum because of the self-inhibitor present in such spores. Low germination levels in the water controls were desired so that maximum stimulatory effects would be emphasized. The duration of the germination test was 2.5 h at 22–24 °C. Four loops of spores were taken from each concentration, and two counts of 100 spores each were made from each drop. Germination percentages were thus based on 800 spores, usually counted by two observers. Active compounds usually stimulated germination at several concentrations in the 10–1000 μL/L range. When one compound seemed much more effective than others, it was used as a standard and all other compounds were rated against it. The rating was calculated by the formula

$$\text{rating} = (\%\ \text{germination at optimum concentration of test compound} - \%\ \text{germination of water controls})/(\%\ \text{germination of standard stimulator} - \%\ \text{germination of water controls}) \times 100$$

Compounds used were obtained from commercial sources. Except for α- and β-pinene (94%, 90% pure) and octyl sulfide (92% pure), all exceeded 95% purity as determined by gas chromatography on Poly I-110 columns. Stigmasterol (95%) was not chromatographed.

When the effects of temperature on germination stimulation were studied, a series of incubators was used. Uredospores were dispersed by a microcyclone device and allowed to settle on pieces of Millipore filter in a glass cylinder. Plastic Petri dishes (50 mm) containing 5.0 mL of 1% Bacto agar with or without stimulator were placed in the incubators for about 1 h to equilibrate before the start of the experiments. The pieces of Millipore filter were placed on damp paper towels in a large Petri dish and distributed to the agar plates in the various incubators. The Millipore filter sections were inverted on the surface of the agar, rubbed lightly with forceps, and peeled off, leaving the uredospores on the agar. Spore density was heavy, with spores only a few spore diameters apart, again to induce self-inhibition. At the end of the germination time, 2.5 h, the lids of the Petri plates were removed and the dishes placed in a glass desiccator containing 0.5 L of 37% formaldehyde solution to stop germination.

RESULTS

Earlier experiments indicated that uredospores of *P. punctiformis* were not effectively stimuated by nonanal or β-ionone, as were those of many other species. However, 5-methyl-2-hexanone stimulated germination up to 83% and was used as the standard in further studies. 2-Heptanone was the most effective of the linear five- to nine-carbon ketones and was 97% as promotive as the standard (Table I). Both 2-heptanone and the standard were most effective at 50 μL/L. The five-, eight-, and nine-carbon linear ketones and the unsaturated or branched ketones had ratings less than 50.

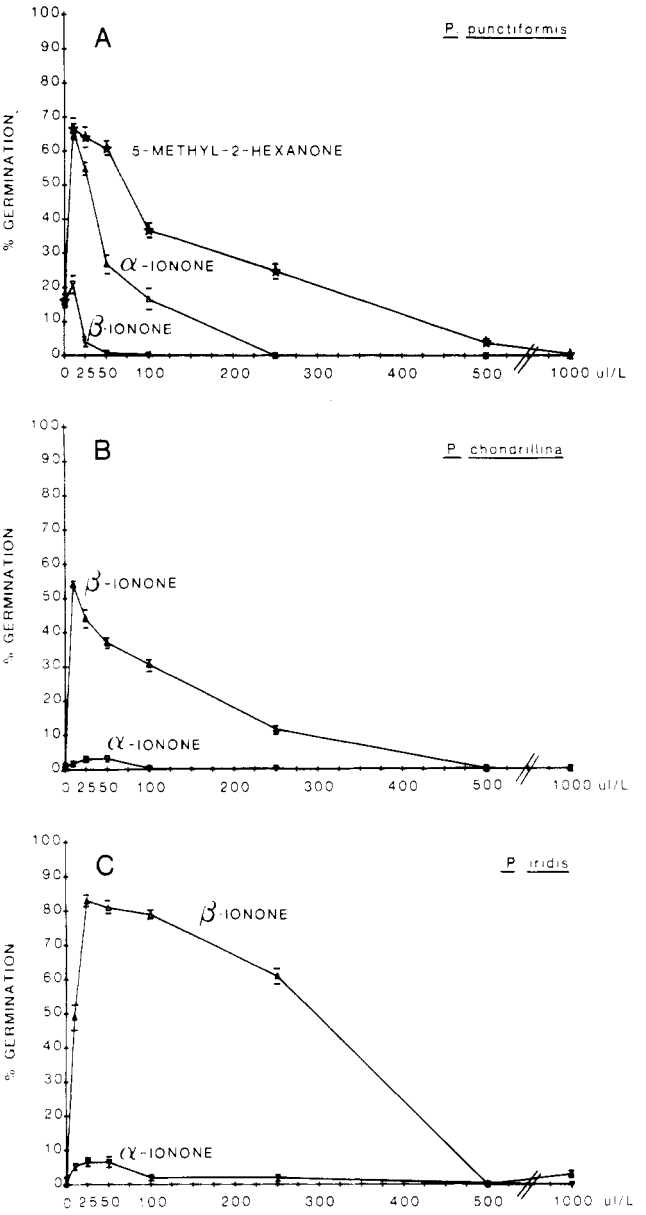

Figure 1. Effect of concentration of stimulators on germination of rust uredospores for 2.5 h at 22–23 °C. (A) 5-Methyl-2-hexanone (★), α-ionone (△), and β-ionone (▽) on *P. punctiformis*. Germination values above 25% are significantly different from controls at $P = 0.01$. (B) α-Ionone (▽) and β-ionone (△) on *P. chondrillina*. Values above 10% are significantly different from controls at $P = 0.01$. (C) α-Ionone (▽) and β-ionone (△) on *P. iridis*. Values above 20% are significantly different from controls at $P = 0.01$. Bars (—) = ± standard error of means.

Of the cyclic ketones, β-ionone was much less active (0) than α-ionone (27) and 1-phenyl-2-butanone (54) (Table I). The *d* isomer of carvone had a rating of 40 at 100 μL/L, but the *l* isomer was virtually inactive. The α- and β-pinenes, cyclic hydrocarbon compounds, were inactive. Nonyl mercaptan (42) was active. 5-Methyl-2-hexanone was clearly the most effective of all those compounds studied and listed in Table I.

5-Methyl-2-hexanone, from 50 to 500 μL/L (Figure 1A), was at least twice as active as α-ionone. α-Ionone was several times more active than β-ionone at all active con-

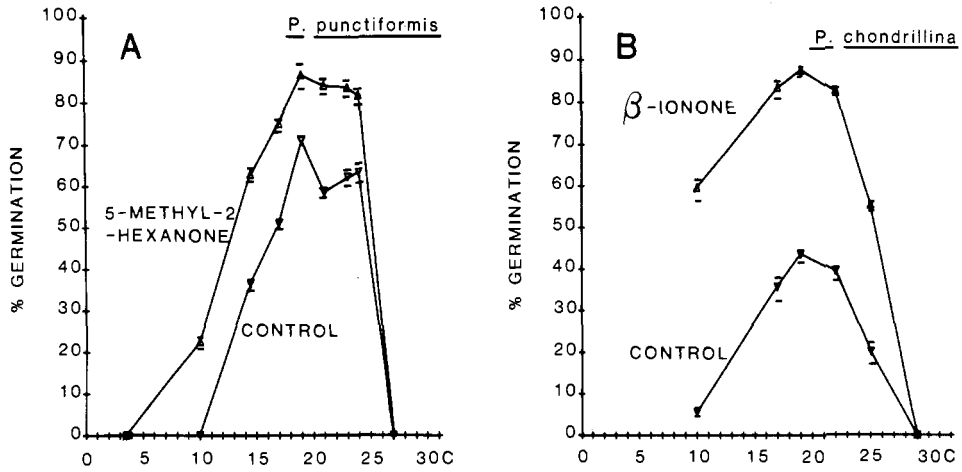

Figure 2. Effect of temperature on chemical stimulation of uredospore germination. (A) 100 μL/L 5-methyl-2-hexanone (△); 1% water agar (▽); 2 h at 3–27 °C. (B) 100 μL/L β-ionone (△); 1% water agar (▽); 2 h at 10–29 °C. Bars (—) = ± standard error of means.

Table I. Effect of Volatile Chemicals on Germination of Uredospores of *P. punctiformis* Compared to 50 μL/L 5-Methyl-2-hexanone as the Standard (Germination Time 2.5 h; Temperature 22-23 °C)

compound	concn,[a] μL/L	rating[b]
5-methyl-2-hexanone	50	100
ketones		
linear, saturated		
2-pentanone	50	24
2-hexanone	50	54
2-heptanone	50	97
2-octanone	50	37
2-nonanone	100	0
unsaturated or branched		
6-methyl-5-hepten-2-one	50	47
5-hexen-2-one	50	7
cyclic		
β-ionone	25	0
α-ionone	25	27
1-phenyl-2-butanone	25	54
trans-4-phenyl-3-buten-2-one	50	0
d-carvone	100	40
l-carvone	25	4
miscellaneous		
α-pinene	25	0
β-pinene	50	2
n-octyl cyanide	25	0
nonyl thiocyanate	25	7
nonyl mercaptan	25	42

[a] Concentration in μL/L at which maximum germination occurred, over the range 0–1000 μL/L. [b] Rating = (% germination at optimum concentration − % germination of water control)/(% germination of stimulator control − % germination of water control) × 100.

centrations studied. Maximum germination with this spore lot was 65% with 10 μL/L 5-methyl-2- hexanone or α-ionone.

The most effective stimulator, 5-methyl-2-hexanone, was active over temperatures ranging from 10 to 25 °C (Figure 2A). At 3 and 27 °C, virtually no germination of uredospores was observed.

Stimulator studies also were carried out on uredospores of *P. chondrillina*, a pathogen of rush skeleton weed, *Chondrilla juncea*. In this series of experiments, β-ionone at 10 μL/L was used as the standard.

Of the linear ketones studied (Table II), 2-heptanone at 250 μL/L was most active, with a rating of 124. 2-Hexanone (1000 μL/L) and 2-octanone (100 μL/L) were active with ratings of 59 and 84, respectively. 2-Pentanone (500 μL/L) and 2-nonanone (100 μL/L) were less active with ratings of 8 and 49.

Table II. Effects of Volatile Chemicals on the Germination of Uredospores of *P. chondrillina*, Compared to Germination on 10 ppm of β-Ionone as the Standard (Germination Time 2.5 h at 22-23 °C)

compound	concn,[a] μL/L	rating[b]
β-ionone	10	100
ketones		
linear, saturated		
2-pentanone	500	8
2-hexanone	1000	59
2-heptanone	250	124
2-octanone	100	84
2-nonanone	100	49
unsaturated or branched		
5-methyl-2-hexanone	250	161
6-methyl-5-hepten-2-one	100	91
cyclic		
α-ionone	25	3
d-carvone	25	110
l-carvone	100	61
alcohols		
2-octanol	100	18
2-nonanol	25	14
miscellaneous		
n-octyl sulfide	1000	25
n-octyl thiocyanate	250	42
decanenitrile	50	76
stigmasterol	1000	73

[a] Concentration in μL/L at which maximum germination occurred, over the range 0–1000 μL/L. [b] Rating = (% germination at optimum concentration − % germination of water control)/(% germination of stimulator control − % germination of water control) × 100.

Of the branched ketones, 5-methyl-2-hexanone also was more active than the β-ionone standard (100) and had a rating of 161 at 250 μL/L. 6-Methyl-5-hepten-2-one was very active, with a rating of 91 at 100 μL/L.

Three cyclic ketones besides β-ionone were tested (Table II). Of these α-ionone was inactive, with a rating of 3 at 25 μL/L. The carvones were more active. *d*-Carvone was slightly more active than the standard, with a rating of 110 at 25 μL/L. *l*-Carvone was less active with a rating of 61 at 100 μL/L.

The alcohols tested had little activity. Among the miscellaneous compounds, decanenitrile (rating 76 at 50 μL/L) and stigmasterol (rating 73 at 1000 μL/L) were active (Table II).

The marked effect of β-ionone over that of α-ionone on *P. chondrillina* is shown in Figure 1B. β-Ionone was more stimulatory from 25 to 250 μL/L, with maximum germination of 44% at 25 μL/L in this experiment. α-Ionone

Table III. Effect of Volatile Chemicals on Germination of Uredospores of *P. iridis*, Compared to Germination on 50 μL/L β-Ionone as the Standard (Germination Time 2.5 h at 22–23 °C)

compound	concn,[a] μL/L	rating[b]
β-ionone	50	100
ketones		
linear, unsaturated, or branched		
5-methyl-2-hexanone	25	7
6-methyl-5-hepten-2-one	25	0
cyclic		
α-ionone	25	4
1-phenyl-2-butanone	25	64
trans-4-phenyl-3-buten-2-one	25	0
d-carvone	25	68
l-carvone	25	0
hexanophenone	50	0
aldehydes		
1-nonanal	50	4

[a] Concentration in μL/L at which maximum germination occurred, over the range 0–1000 μL/L. [b] Rating = (% germination at optimum concentration − % germination of water control)/(% germination of stimulator control − % germination of water control) × 100.

increased germination only slightly above controls and only at 25 and 50 μL/L, with maximum germination less than 5%. As shown in Figure 2B, β-ionone was an effective stimulator of *P. chondrillina* and stimulated germination 2-fold over a temperature range of 10–25 °C.

The differential response to isomers of ionone was observed first in spores of *P. iridis* and this was the main reason for studying this species. The most effective compound on uredospores of *P. iridis* appeared to be β-ionone; hence, this compound at a concentration of 50 μL/L was used as the standard for the compounds reported in Table III. α-Ionone was nearly inactive. The linear aldehydes or ketones tested were either inactive or not appreciably active, including 5-methyl-2-hexanone and 6-methyl-5-hepten-2-one, which were active on *P. punctiformis* and *P. chondrillina*. Of the cyclic ketones, 1-phenyl-2-butanone (25 μL/L) was active, with a rating of 64. Uredospores of *P. iridis* and *P. punctiformis* were both stimulated by 1-phenyl-2-butanone but not by *trans*-4-phenyl-3-buten-2-one. These compounds may be considered structurally related to the ionones.

A marked difference occurred between the two isomers of carvone. The *l*-carvone (25 μL/L) was inactive, rating 0, while *d*-carvone (25 μL/L) was active with a rating of 68 (Table II).

All three species were more stimulated by *d*-carvone than by *l*-carvone. *P. punctiformis* and *P. iridis* did not respond appreciably to the *l*-carvone isomer. *P. chondrillina* responded about as well to *d*-carvone as to β-ionone, but *l*-carvone also was fairly active (Table I–III).

The great difference in response of *P. iridis* to α- and β-ionones is shown in Figure 1C. Stimulation by α-ionone was less than 5% for the entire concentration range. β-Ionone stimulated germination as much as 80% at 50 μL/L and over 20% for the concentration range of 25–500 μL/L.

A few compounds also were tested on *U. trifolii-repentis*, which infects red clover, *Trifolium pratense*. Although no detailed studies were made, several compounds were tested and are listed in Table IV. Uredospores of *U. trifolii-repentis* responded best to β-ionone and moderately well to α-ionone and octyl cyanide. The carvone isomers were inactive. The responses of this rust to chemical stimulators were not so unusual as to warrant further testing.

Table IV. Effect of Volatile Chemicals on Germination of Uredospores of *U. trifolii-repentis* for 3 h at 22–23 °C

compound	concn,[a] μL/L	% germination	
		control	treated
β-ionone	20	1	90[b]
α-ionone	10	1	47
d-carvone	10	23	0
l-carvone	10	1	0
octyl cyanide	25	0	45[b]
6-methyl-5-hepten-2-one	10	5	9
1-nonanol	10	3	6
nonyl mercaptan	500	4	15

[a] Concentration in μL/L at which maximum germination occurred, over the range 0–1000 μL/L. [b] Significant from the control at $P = 0.01$.

DISCUSSION

In previous papers (French and Gallimore, 1971; French et al., 1975a,b, 1977) we had shown that several species of uredospores respond best to one of two compounds, or two types of compounds, nonanal (or nonanol) or β-ionone. The efficacy of these two compounds could be most dramatically shown by the ability of certain species to germinate "in pustule" in response to the chemicals when diseased plants were placed in dew chambers with small amounts of these volatile compounds. Structure–activity studies with spores floated on water or tested "in pustule" indicated that β-ionone was most effective for stimulating uredospores of *Uromyces phaseoli* (French et al., 1977) and nonanol for those of *Puccinia graminis* var. *tritici* (French and Gallimore, 1971).

In this study, 5-methyl-2-hexanone was found to be the most effective compound for *P. punctiformis* and *P. chondrillina*. Recently Charudattan et al. (1981) have shown that β-ionone, 2-hexanone, 2-heptanone, α-ionone, 5-methyl-2-hexanone, 1-octanol (in order of relative effectiveness), and others were effective germination stimulators of uredospores of *Uromyces pontederiae*.

5-Methyl-2-hexanone appeared most effective with *Uredo eichhorniae*, but a rather high concentration, 500 μL/L, was required. These rusts, which are pathogens of water weeds, apparently require stimulators for any appreciable amount of germination. The differential responses of the above rusts are good examples of the degree of species diversity which exists in the response of uredospores to these naturally occurring volatile compounds. It should be noted also that of those species which preferentially respond to ketones, such as *U. phaseoli* (French et al., 1977) and *P. punctiformis* and *P. chondrillina*, all responded best to 2-heptanone when tested for response to the linear five-to nine-carbon ketones. Although these species responded best to 2-heptanone, a remarkable difference in response to α- and β-ionones was observed. Whereas *U. phaseoli* responded almost equally well to both α- and β-ionones, *P. chondrillina* and *P. iridis* were stimulated only by β-ionone. α-Ionone was very much more effective on *P. punctiformis* than was the β isomer. The difference between the α and β forms is the position of a double bond, which is conjugated in the β form.

Leppik et al. (1972) have reported a distinct difference between α- and β-ionones as inhibitors of conidial germination in *Peronospora tabacina*. β-Ionone and quiesone (5-isobutyroxy-β-ionone), the latter identified from infected tobacco leaves, inhibited conidial germination at ED50's of 0.15 and 0.0001 ppm, respectively. α-Ionone was not inhibitory.

As shown by this and previous research, the chemical stimulation of uredospores of various rust species seem to

fall into two arbitrary levels or types of activity. The first level consists of compounds with rather low to moderate germination ratings, perhaps as much as 50% or greater, induced by a broad spectrum of chemicals with diverse structures. For *P. punctiformis*, such compounds as 2-hexanone, 6-methyl-5-hepten-2-one, and nonyl mercaptan might be included. For *P. chondrillina*, 2-octanone, 2-nonanone, *l*-carvone, decanenitrile, and stigmasterol might be considered in the first level.

The second level of activity consists of compounds which are very effective stimulators and includes the compounds used as standard stimulators, some of which also may be capable of stimulating germination of uredospores in pustules, such as β-ionone and nonanal.

This research has extended the range of biological activity of flavor compounds on rust spores, showing that four additional rust species respond to volatile germination stimulators. Of these, two species, *P. punctiformis* and *P. chondrillina* respond best to 5-methyl-2-hexanone. Elsewhere, Charudattan et al. (1981) have shown 5-methyl-2-hexanone to be most effective on uredospores of *U. eichhorniae*. Of all the compounds studied since identification of 1-nonanal as an endogenous rust spore stimulator (French and Weintraub, 1957; Rines et al., 1974), three now can be considered as most effective when considering the maximum percent germination of various species (but not the most effective minimum concentration of compound required). These are nonanol, β-ionone, and, with this report, 5-methyl-2-hexanone. An unusual degree of structural specificity has been found, indicated in the differential responses to α- and β-ionones and *d*- and *l*-carvones. Specificity studies are considered an integral part of understanding mechanism of action and of adapting the unusually sensitive action of the flavor compounds on the germination mechanism of fungal spores to solving practical problems of pest control. Two of the rust species, *P. punctiformis* and *P. chondrillina*, have been considered as possible biocontrol agents for the noxious weeds, Canada thistle, *Cirsium arvense*, and rush skeleton weed, *Chondrilla juncea*. The ability to stimulate germination over a broad temperature range could be useful for inducing initial phases of a field infection.

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Registry No. 5-Methyl-2-hexanone, 110-12-3; 2-pentanone, 107-87-9; 2-hexanone, 591-78-6; 2-heptanone, 110-43-0; 2-octanone, 111-13-7; 2-nonanone, 821-55-6; 6-methyl-5-hepten-2-one, 110-93-0; 5-hexen-2-one, 109-49-0; β-ionone, 79-77-6; α-ionone, 127-41-3; 1-phenyl-2-butanone, 1007-32-5; *trans*-4-phenyl-3-buten-2-one, 1896-62-4; *d*-carvone, 2244-16-8; *l*-carvone, 6485-40-1; α-pinene, 80-56-8; β-pinene, 127-91-3; *n*-octyl cyanide, 2243-27-8; nonyl thiocyanate, 25681-48-5; nonyl mercaptan, 1455-21-6; 2-octanol, 123-96-6; 2-nonanol, 628-99-9; *n*-octyl sulfide, 2690-08-6; *n*-octyl thiocyanate, 19942-78-0; decanenitrile, 1975-78-6; stigmasterol, 83-48-7; hexanophenone, 942-92-7; nonanol, 28473-21-4.

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