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Extractable Amounts of *trans*-Resveratrol in Seed and Berry Skin in *Vitis* Evaluated at the Germplasm Level

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Extractable amounts of resveratrol in berry skins and seeds were studied in 120 grape (*Vitis*) germplasm cultivars during two consecutive years to determine the distribution of resveratrol among the main grape genotypes. Interspecific rootstock cultivars had much higher extractable amounts of resveratrol in skin and seed than all other grape genotypes studied in both years. Extremely high extractable amounts of resveratrol in berry skins [>100 μg g^{-1} of skin fresh weight (FW)] and seeds (>20 μg g^{-1} of seed FW) were observed on two rootstock cultivars obtained from hybrids of *V. monticula* × *V. riparia*. Extractable amounts of resveratrol in berries of rootstock cultivars that are the descendants of *V. riparia* were also very high. The cultivated European type (*V. vinifera*) cultivars and their hybrids with *V. labrusca* had relatively low levels of extractable resveratrol in berry skin and seed, and the extractable amounts of resveratrol in berry skin and seeds were, with a few exceptions, <2 μg g^{-1} of skin or seed FW. Extractable amounts of resveratrol in berry skin and seeds were closely related with fruit traits or purpose of uses and climate. Significantly higher extractable amounts of resveratrol in berry skin were found in seeded cultivars than in seedless ones, in both berry skin and seeds in winemaking grapes than in table grapes, and in red grapes than in green ones. Moreover, rainfall during fruit development resulted in higher extractable amounts of resveratrol in berry skin, whereas resveratrol synthesis and accumulation in grape seeds were not related to climate change.

KEYWORDS: Resveratrol; grape germplasm; fruit traits

INTRODUCTION

trans-Resveratrol (3,5,4′-trihydroxystilbene) is one of the major stilbene phytoalexins, originally identified as an active ingredient of oriental folk medicines used for treatment of a wide variety of diseases (*1, 2*). This compound has been found in at least 72 plant species distributed among 31 genera and 12 families (*3*), and a number of these are components of the human diet, for example, grapes, wine, grape juice, cranberries (*4*), peanuts (*5*), and chocolate and cocoa (*3*). Grapes and grape products, however, are considered to be the most important human dietary sources of resveratrol (*6*−*8*).

The interest in resveratrol in grape was originally sparked by epidemiological studies indicating an inverse relationship between moderate consumption of red wine over a long period of time and risk of coronary heart disease, the so-called "French paradox" (*9*). This biological attribute has been ascribed to resveratrol (*10*), and several kinds of evidence have accumulated in support of resveratrol's pharmacological activities. Resveratrol's reported biological attributes include anti-inflammatory (*11*), cardioprotection (*12*), cancer chemopreventive (*13*), and antioxidant properties (*14*) and inhibition of platelet aggregation (*10*).

Resveratrol's synthesis can be accomplished in the laboratory via the Heck reaction (*15*), but the use of synthetic food additives in the food industry is often severely restricted. Consequently, there is more and more interest in natural resveratrol extracted from plants, especially from grape and grape products.

The grape is the world's second largest fruit crop, with >66.41 million metric tons produced in 2005 (FAO STAT Database at www.fao.org). About 13.4% of the total grapes harvested are for fresh consumption (table grapes), whereas 86.6% of the crop is processed, especially for winemaking (*16*). Grapes cultivated throughout the world today mainly belong to three types, the European type (*Vitis vinifera* L.), the American bunch type (*Vitis labrusca* L. and its derivatives, especially the hybrids obtained from *V. labrusca* and *V. vinifera*), or the Muscadine type (*Vitis rotundifolia* Michx). All of these grape germplasm resources can provide abundant natural resveratrol products. Therefore, it is important to evaluate resveratrol content in grape germplasm in order to utilize those germplasm resources to produce resveratrol or in breeding programs to obtain new grape cultivars with high levels of resveratrol in their berries.

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Table 1. Grape Cultivars Used in This Study

genotype group[a]	no. of cultivars	cultivar[b]
table grape of LV	52	Beniyamabiko (1), Benizawa (2), Benizuiho (3), Bennifuji (4), Black Olimpia (5), Canadice (6), Catawba (7), Delaware (4×) (8), Guixiangyi (9), Himrod (10), Jifeng (11), Jingchao (12), Kangtai (13), Kunitachi Seedless (14), Mars Seedless (15), Pondicherry (16), Queenora Seedless (17), Ryuho (18), Swenson Red (19), Takasuma (20), Tano Red (21), Triumph (22), Vehava 180 (23), Venus (24), Yigawa 1014 (25), Yigawa 1015 (26), Yigawa 1025 (27), Yigawa 1050 (28), Yigawa 1055 (29), Yigawa 1060 (30), Beni Sajku (31)†, Beniizu (32)†, Fujiminori (33)†, Honey Red (34)†, Hongboduo (35)†, Hyuga (36)†, Izunishiki (37)†, Kyoho (38)†, Rhodo Berry (39)†, Roudingxiang (40)†, Ruby Niagara (41)†, Urbana (42)†, Vehava540 (43)†, Violet Vehara (44)†, Wase Takasumi (45)†, Fenghou (46)§, Harata 314 (47)§, Jingya (48)§, Jingyou (49)§, Premium (50)§, Red Queen (51)§, White Olympia (52)§
juice grape of LV	1	Honey Juice (53)§
wine grape of LV	1	Super Hamburg (54)§
table grape of V	31	Centennial Seedless (55), Early Muscat (56), Gloria Hungariae (57), Gros Colman (58), Jingdajing (59), Jingkejing (60), Jingxiu (61), Jingzaojing (62), Kuratsufuri (63), Misket Dounvaski (64), Muscat Hamburg (65), Fenghuang 51 (66), Red Globe (67), Ruby Seedless (68), Su161 (69), Suffolk (70), Thompson seedless (71), Zaoyu (72), Fenniu (73)†, Guibao (74)†, Hiro Hamburg (75)†, Jingyu (76)†, Jingzijing (77)†, Otilia (78)†, Wajisilibaiyu (79)†, Zaomanao (80)†, Xiangfei (81)§, Huaze Lizamate (82)§, Queen of Vineyards (83)§, Shiyaira (84)§, Superior Seedless (85)§
wine grape of V	21	Bujiesuli (86), Carigane (87), French Blue (88), Meichun (89), Merlot (90), Semillon (91), Su162 (92), Ugni Blanc (93), White Suntory (94), Wuyuezi (95), Zexiang (96), Baiyu (97)†, Cabernet Franc (98)†, Chardonnay (99)†, Guoho2 (100)†, Italian Riesling (101)†, Pannoniavinesa (102)†, Cabernet Gernischet (103)§, Lion Riesling (104)§, Suntory (105)§, Yan73 (106)§
wine grape of VA	3	Beichun (107), Beihong (108), Beiquan (109)
juice grape of TV	2	Beifeng (110)†, Beizi (111)†
juice grape of LA	1	Russia Concord (112)
rootstock grape of RR	1	101-14 (113)
rootstock grape of BR	1	5A (114)
rootstock grape of AR	1	ARH2 (115)
rootstock grape of MR	3	188-8 (116), Zhi 166 (117), Zhi 168 (118)
rootstock grape of LR	1	Beta (119)§
Chinese wild grape species Ad	1	Yanshan (120)

[a] LV, hybrids between *V. labrusca* and *V. vinifera*; V, *V. vinifera*; VA, *V. vinifera* × *V. amurensis*; TV, *V. thunbergii* × *V. vinifera*; LA, *V. lubrusca* × *V. amurensis*; RR, *V. riparia* × *V. rupestris*; BR, *V. berlandier* × *V. riparia*; AR, *V. amurensis* × *V. riparia*; MR, *V. Monticola* × *V. riparia*; LR, *V. labrusca* × *V. riparia*; Ad, *V. amurensis* var. *dissecta*. [b] Number in parentheses following the cultivar indicates the sample order; † indicates used in 2003 only; § indicates use in 2004 only.

In grape berries resveratrol is primarily synthesized and located in the skin and seed cells with little or none in the fruit flesh (*7*, *8*). Although there have been several studies of resveratrol in grape berry skins and seeds (*6*−*8*), none has yet investigated resveratrol in berry skins and seeds at the grape germplasm level. Germplasm resources are very rich, and there are at least 70 species in the genus *Vitis* (*16*). Moreover, cultivars are numerous, with >10000 in the world, due to a long history of cultivation and an extensive geographical distribution (*16*). Grape germplasm resources should play an important role in resveratrol synthesis, which may be genetically controlled. The purpose of the present study is to explore the variations in extractable amounts of resveratrol in skins and seeds in grape germplasm. This should provide basic data (1) for further study of the genetic basis of grape resveratrol metabolism, (2) to find new medicinal resources, and (*3*) to exploit the grape germplasm with high levels of resveratrol in breeding programs to obtain new cultivars rich in resveratrol.

MATERIALS AND METHODS

Plant Material. There were 120 grape cultivars used in this study in 2003 and 2004, and 70 were studied in two successive years. The total included 52 table grapes, 1 juice grape, and 1 wine grape hybrid between *V. labrusca* and *V. vinifera*, 21 wine grapes and 31 table grapes of *V. vinifera*, 3 wine grape hybrids of *V. vinifera* × *V. amurensis*, 2 juice grape hybrids of *V. thunbergii* × *V. vinifera*, 1 juice grape hybrid of *V. amurensis* × *V. lubrusca*, 7 rootstock hybrids from *V. amurensis* × *V. riparia* (1), *V. berlandier* × *V. riparia* (1), *V. riparia* × *V. lubrusca* (1), *V. monticula* × *V. riparia* (3), and *V. riparia* × *V. rupestris* (1), and a Chinese wild grape species *V. amurensis* var. *dissecta* (**Table 1**). All samples were collected from the Germplasm Repository for grapes in the Institute of Botany of the Chinese Academy of Sciences located in Beijing. All of the cultivars were planted in the spring of 1993. The vines, trained to bilateral cordons, were spaced 1.5 m apart within the row and 2.5 m apart between rows with a north−south row orientation. All were subjected to the same management practices, such as irrigation, fertilization, soil management, pruning, and disease control.

Grapes were hand-harvested from mid-July to late September at the ripening stage of each cultivar. The berry ripening stage was evaluated on the former year's ripening date and as judged from seed color change to dark brown without senescence of berry tissue. Berries were sampled from three clusters, randomly chosen in thee vines of each cultivar as three replications. The samples were taken to the laboratory, and the skins and seeds were separated by hand immediately. The skins and seeds were then frozen in liquid nitrogen, ground to a powder, and then stored at −40 °C.

Extraction of Resveratrol from Skins and Seeds. *trans*-Resveratrol was extracted according to the method of Li et al. (*17*). Three gram samples were ground using a porcelain mortar and pestle in 15 mL of extraction solvent (ethyl acetate for berry skins and methanol for seeds; both reagents were of analytical grade and purchased from Beijing Chemical Plant, Beijing, China). The samples were extracted in the dark at 25 °C for 48 h and then centrifuged at 10000*g* for 10 min. The supernatants were evaporated to dryness by rotary vacuum evaporation at 40 °C. Dried samples were then dissolved in 1 mL of methanol and stored at −40 °C. The samples were filtered through a 0.45 μm PTFE membrane filter before resveratrol analysis.

Determination of Resveratrol Concentration. Extractable amounts of resveratrol were analyzed using a Dionex Summit HPLC system including a Dionex P680 pump, a Dionex TCC-100 thermostated

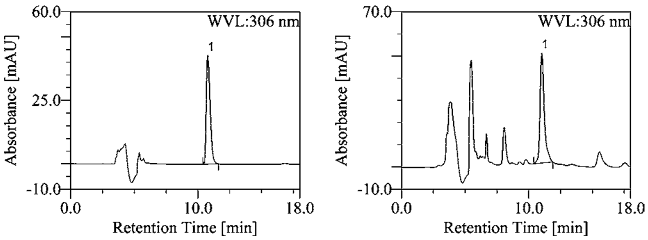

Figure 1. HPLC chromatograms of resveratrol from standard solution (left) and grape berry sample (right). Peak 1 is *trans*-resveratrol.

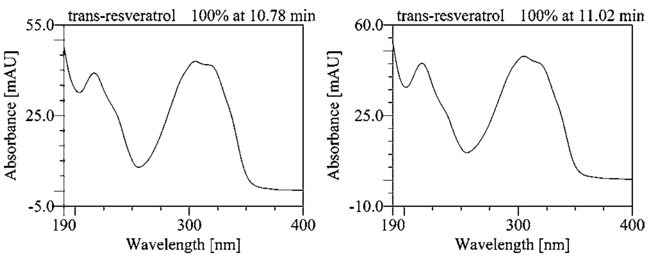

Figure 2. Scanning spectrograms (190–380 nm) of resveratrol from standard solution (left) and grape berry sample (right).

column compartment, and a Dionex PDA-100 detector (Dionex Corp., Sunnyvale, CA). The resveratrol was separated on an Inertsil ODS-3 column (250 mm L × 4.6 mm i.d., 5 μm particle size, purchased from GL Sciences Inc., Tokyo, Japan) and a guard column cartridge (Sunchrom C18 cartridge from The Great Eur-asia Science & Development Co. Ltd., Beijing, China) maintained at 25 °C. A 10 μL sample solution was eluted with 40% acetonitrile (gradient grade, Sigma-Aldrich Chemie GmbH, Steinheim, Germany) at a flow rate of 0.6 mL min^{-1}. *trans*-Resveratrol was monitored at 306 nm wavelength. HPLC chromatograms of resveratrol from a standard solution (Sigma-Aldrich, Inc., St. Louis, MO) and a grape berry sample are shown in **Figure 1**. The spectrum from the PDA-100 confirmed that the peak of the grape berry sample showing the same retention time as that of standard sample on the HPLC chromatograms was *trans*-resveratrol (**Figure 2**). The Chromeleon chromatography management system (version 6.50) was used to integrate peak areas according to external standard solution calibrations. Calibration curves were established by plotting the area of peaks against different concentrations of *trans*-resveratrol. The quantitation limit was about 0.011 $\mu g\ g^{-1}$. Regression equation: $y = 0.5468x - 0.4941$, $R^2 = 0.9957$, linear range covering from 0.02 to 70 $\mu g\ g^{-1}$. Regression equation: $y = 0.5073x + 10.775$, $R^2 = 0.9073$, linear range covering from 70 to 390 $\mu g\ g^{-1}$.

Statistical Analysis. Data for each cultivar in each year were averages of three replications. Mean values were used as estimated cultivar values for analyzing the variations of extractable amounts of resveratrol in skins and seeds of the major examples of grape germplasm. Cultivar variations in extractable amounts of resveratrol were analyzed by S-Plus 2000 (MathSoft Inc., Cambridge, MA). The boxplots, statistical figures for describing distribution of data, were made to display range, median, and distribution density of variables in sample size (*18*). The medians of the data are indicated by the horizontal line in the interior of the box. The height of the box is equal to the interquartile distance, which is the difference between the third quartile of the data and the first quartile. The whiskers (the dotted lines extending from the top and bottom of the box) extended to a distance 1.5 × the interquartile distance from the center. Approximately 99% of the data fall inside the whiskers. Data outside these whiskers are indicated by horizontal lines.

Using the *F* tests, a total of 106 grape cultivars of the most important two commercial grape groups, *V. vinifera* and hybrids between *V. labrusca* and *V. vinifera*, were used to analyze the relationship of extractable resveratrol amounts in berry skin and seed and the different fruit traits or purpose of use. For studying the stability of extractable amounts of resveratrol in the skins and seeds between the two years, only the 70 grape cultivars that were studied in two successive years were analyzed by the *F* tests. The *F* tests were based on the linearly independent pairwise comparisons among the estimated marginal means. The univariate analysis of variance of nested design was performed using the General Linear Model function of SPSS 10.0 for Windows (SPSS Inc., Chicago, IL).

RESULTS

Genotypic Variation of Extractable Amounts of Resveratrol in Grape Berry Skin. The frequency distribution and median of extractable amounts of resveratrol in grape berry skins were similar in the two years (**Figure 3**). The rootstock cultivars had much higher amounts of extractable resveratrol in skin than all other grape genotypes in this study in both years. Extractable amounts of resveratrol in the skin of rootstock cultivars ranged from 7.9 to 182.5 $\mu g\ g^{-1}$ of skin fresh weight (FW) with a median of 40.92 $\mu g\ g^{-1}$ of skin FW in 2003 and from 17.3 to 356.1 $\mu g\ g^{-1}$ of skin FW with a median of 114.9 $\mu g\ g^{-1}$ skin FW in 2004, respectively. The extractable amounts of resveratrol in the skin of rootstock cultivars varied significantly with their genetic backgrounds. The highest amounts of extractable resveratrol in skin were found in ‘Zhi 168’, a hybrid of *V. monticula* × *V. riparia*, reaching 182.5 and 356.1 $\mu g\ g^{-1}$ of skin FW in 2003 and 2004, respectively. Another hybrid of *V. monticula* × *V. riparia*, ‘Zhi 166’, also produced high amounts of extractable resveratrol in berry skin, reaching 127.5 and 217.6 $\mu g\ g^{-1}$ of skin FW in 2003 and 2004, respectively. The extractable amounts of resveratrol in skins of ‘Beta’ (a hybrid from *V. riparia* × *V. lubrusca*), ‘188-8’ (a hybrid from *V. monticula* × *V. riparia*), and ‘101-14’ (a hybrid from *V. riparia* × *V. rupestris*) were also higher, reaching 49.63 and 32.21 $\mu g\ g^{-1}$ of skin FW in 2003 (there were no ‘Beta’ data in 2003) and 230.52, 114.89, and 59.29 $\mu g\ g^{-1}$ of skin FW in 2004, respectively. The lowest extractable amounts of resveratrol in berry skin were in ‘ARH2’, a hybrid of *V. amurensis* × *V. riparia*, in 2003 and in ‘5A’, a hybrid of *V. berlandier* × *V. riparia*, in 2004. These extractable amounts of resveratrol were 7.9 and 17.3 $\mu g\ g^{-1}$ of skin FW for ‘ARH2’ and ‘5A’, respectively.

The extractable amounts of resveratrol in berry skin of cultivated cultivars, including the wine and table grape cultivars of *V. vinifera* and interspecific *V. labrusca* and *V. vinifera* hybrid cultivars, were much lower than previously found for the rootstocks. Moreover, extractable amounts of reseveratrol showed continuous variation and presented an abnormal distribution with a median much lower than their average (**Figure 3**). Extractable reseveratrol amounts of most cultivated cultivars of *V. vinifera* and interspecific hybrid cultivars between *V. labrusca* and *V. vinifera* were concentrated in the low area in their whiskers of the boxplot in both 2003 and in 2004.

The extractable amounts of resveratrol in berry skin of wine grape cultivars of *V. vinifera* ranged from 0.17 to 3.80 $\mu g\ g^{-1}$ of skin FW with a median of 0.73 $\mu g\ g^{-1}$ of skin FW in 2003 and from 0.01 to 17.4 $\mu g\ g^{-1}$ of skin FW with a median of 0.94 $\mu g\ g^{-1}$ of skin FW in 2004. The cultivar ‘Cabernet Gernischet’ had the highest amounts of extractable resveratrol among the *V. vinifera* wine grape cultivars, reaching 17.4 $\mu g\ g^{-1}$ of skin FW in 2004 (no measurement was made in 2003). Two other cultivars, ‘Merlot’ and ‘Wuyuezi’, also contained higher amounts of extractable resveratrol, 3.80 and 2.65 $\mu g\ g^{-1}$ of skin FW in 2003 and 5.48 and 3.94 $\mu g\ g^{-1}$ of skin FW in 2004, respectively. Several wine grapes with relatively high amounts of extractable resveratrol of *V. vinifera* were ‘Cabernet Franc’ (2.29 $\mu g\ g^{-1}$ of skin FW in 2003), ‘Meichun’ (1.54 and 2.94 $\mu g\ g^{-1}$ of skin FW in 2003 and 2004), ‘Su162’ (1.08 and 1.07 $\mu g\ g^{-1}$ of skin FW in 2003 and 2004).

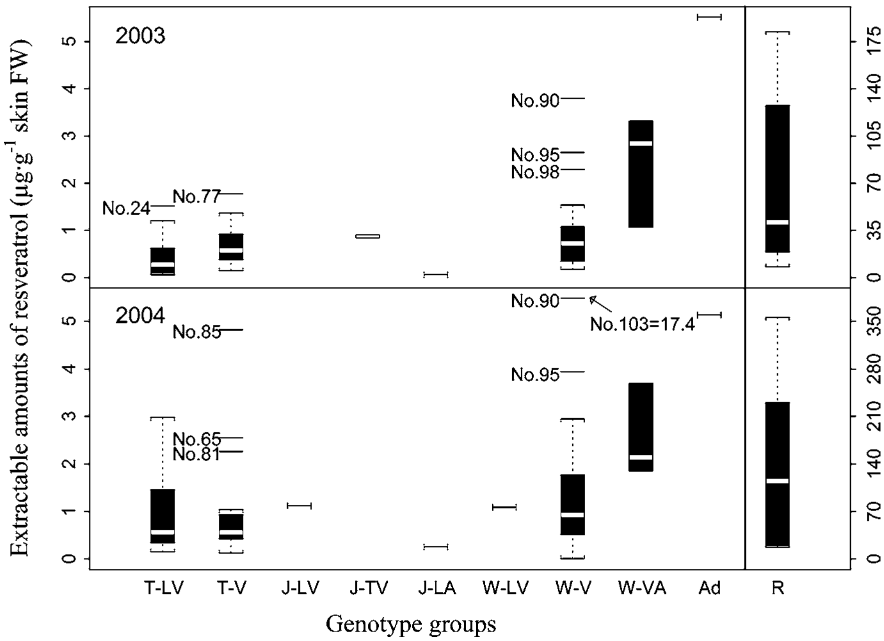

Figure 3. Range and distribution of extractable amounts of *trans*-resveratrol in skin in 2003 (top) and 2004 (bottom). T-LV, table grapes of hybrids between *V. labrusca* and *V. vinifera*; T-V, table grapes of *V. vinifera*; J-LV, juice grape of hybrids between *V. labrusca* and *V. vinifera*; J-TV, juice grape of *V. thunbergii* × *V. vinifera*; J-LA, juice grape of *V. lubrusca* × *V. amurensis*; W-LV, wine grapes of hybrids between *V. labrusca* and *V. vinifera*; W-V, wine grapes of *V. vinifera*; W-VA, wine grapes of *V. vinifera* × *V. amurensis*; Ad, Chinese wild grape species *V. amurensis* var. *dissecta*; R, rootstock cultivars. The numbers just before the lines in the figure represent the accession numbers, which correspond to the same cultivars as in **Table 1**.

The extractable amounts of resveratrol in berry skin of table grape cultivars of *V. vinifera* ranged from 0.14 to 1.77 μg g^{-1} of skin FW with a median of 0.59 μg g^{-1} of skin FW in 2003 and from 0.13 to 4.82 μg g^{-1} of skin FW with a median of 0.56 μg g^{-1} of skin FW in 2004. The seedless cultivar 'Jingzijing', obtained from a cross of Queen of Vineyard × Sultanina Rose by the Institute of Botany of the Chinese Academy of Sciences, had the highest amounts of extractable resveratrol in 2003, reaching 1.77 μg g^{-1} of skin FW (no measurement was made in 2004), whereas the highest extractable resveratrol obtained in 2004 was another seedless cultivar, 'Superior Seedless', reaching 4.82 μg g^{-1} of skin FW (no measurement was made in 2003). Another five cultivars containing higher amounts of extractable resveratrol were cv. 'Fenniu' (1.29 μg g^{-1} of skin FW in 2003), 'Muscat Hamburg' (1.37 and 2.55 μg g^{-1} of skin FW in 2003 and 2004), 'Xiangfei' (2.27 μg g^{-1} of skin FW in 2004), 'Jingxiu' (1.11 and 0.70 μg g^{-1} of skin FW in 2003 and 2004), and 'Zaomanao' (0.96 μg g^{-1} of skin FW in 2003).

The extractable amounts of resveratrol in berry skin of table grape cultivars of the hybrids between *V. labrusca* and *V. vinifera* ranged from 0.06 to 1.52 μg g^{-1} of skin FW with a median of 0.27 μg g^{-1} of skin FW in 2003 and from 0.15 to 2.98 μg g^{-1} of skin FW with a median of 0.57 μg g^{-1} of skin FW in 2004. Two cultivars containing higher levels of resveratrol were 'Venus' and 'Taksuma'. The extractable resveratrol amounts were 1.52 and 1.64 μg g^{-1} of skin FW in 2003 and 2004 for 'Venus' and 1.12 and 2.98 μg g^{-1} of skin FW in 2003 and 2004 for 'Taksuma', respectively. Another five cultivars of the hybrids between *V. labrusca* and *V. vinifera* containing higher amounts of extractable resveratrol were 'Jifeng' (1.21 and 2.00 μg g^{-1} of skin FW in 2003 and 2004), 'Swenson Red' (1.19 and 2.46 μg g^{-1} skin FW in 2003 and 2004), 'Benizawa' (1.07 and 1.91 μg g^{-1} of skin FW in 2003 and 2004), 'Pondicherry' (0.95 and 1.89 μg g^{-1} of skin FW in 2003 and 2004), and 'Jingyou' (1.66 μg g^{-1} of skin FW in 2004).

Regarding the interspecific cultivars for processing use, the extractable amounts of resveratrol in berry skin were higher than the median of the winemaking and table grape cultivars of *V. vinifera* and the table grape cultivars of interspecific hybrids between *V. labrusca* and *V. vinifera*. The three wine grape cultivars, 'Beichun', 'Beiquan', and 'Beihong', selected from hybrids of *V. vinifera* × *V. amurensis* by the Institute of Botany of the Chinese Academy of Sciences, had extractable amounts of reserveratrol of 1.07, 2.85, and 3.31 μg g^{-1} of skin FW in 2003 and 1.86, 2.14, and 3.70 μg g^{-1} of skin FW in 2004, respectively. The only juice grape cultivar, 'Russia Concord', a hybrid between *V. amurensis* and *V. lubrusca*, studied in two successive years in this study, had very low amounts of extractable resveratrol, with only 0.06 and 0.26 μg g^{-1} of skin FW in 2003 and 2004, respectively. The other three interspecific cultivars studied in only 2003 or 2004, presented, however, relatively higher amounts of extractable resveratrol in the berry skin. The extractable amounts of resveratrol were 1.12 μg g^{-1} of skin FW for 'Honey Juice', a hybrid of *V. vinifera* × *V. labrusca* (in 2004), and 0.85 and 0.90 μg g^{-1} of skin FW for 'Beifeng'and 'Beizi', two juice cultivars selected from *V. thunbergii* × *V. vinifera* by the Institute of Botany of the Chinese Academy of Sciences (in 2003).

In *V. amurensis* var. *dissecta*, a Chinese wild species collected in the Germplasm Repository for grapes in the Institute of Botany of the Chinese Academy of Sciences, relatively high amounts of extractable resveratrol in berry skin were found in both years, reaching 5.52 and 5.13 μg g^{-1} of skin FW in 2003 and 2004, respectively.

Genotypic Variation of Extractable Amounts of Resveratrol in Grape Berry Seeds. The frequency distributions of extractable amounts of resveratrol in grape seeds showed continuous variation and presented approximately a normal distribution among almost all grape genotypes tested in the two years (**Figure 4**). The medians of extractable amounts of resveratrol were similar to the means and, except 'Wuyuezi' in 2003, no genotype had a resveratrol concentration outside the whiskers.

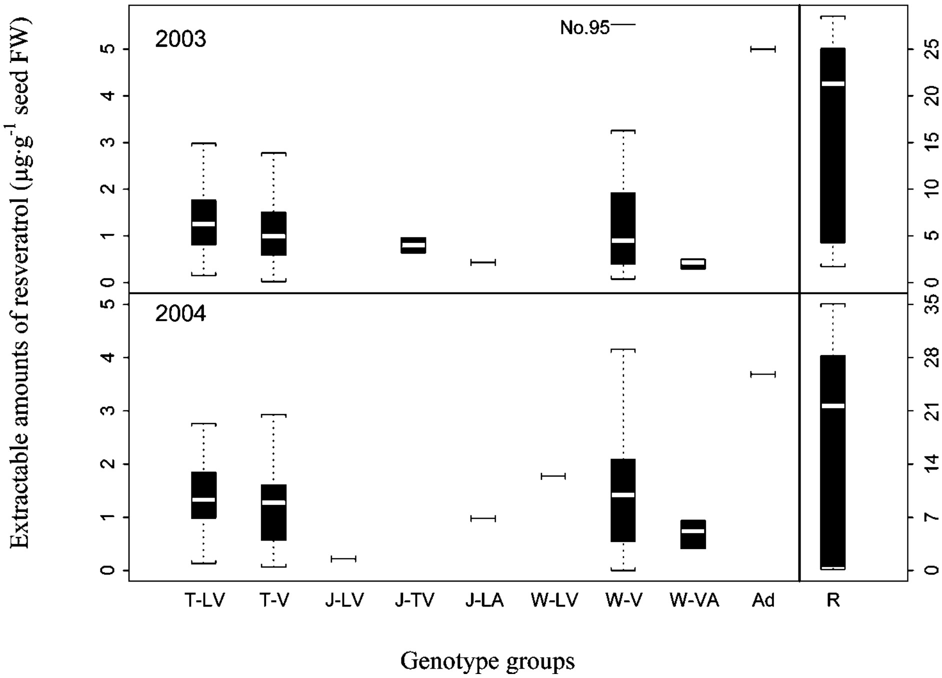

Figure 4. Range and distribution of extractable amounts of *trans*-resveratrol in seed in 2003 (top) and 2004 (bottom). T-LV, table grapes of hybrids between *V. labrusca* and *V. vinifera*; T-V, table grapes of *V. vinifera*; J-LV, juice grape of hybrids between *V. labrusca* and *V. vinifera*; J-TV, juice grape of *V. thunbergii* × *V. vinifera*; J-LA, juice grape of *V. lubrusca* × *V. amurensis*; W-LV, wine grapes of hybrids between *V. labrusca* and *V. vinifera*; W-V, wine grapes of *V. vinifera*; W-VA, wine grapes of *V. vinifera* × *V. amurensis*; Ad, Chinese wild grape species *V. amurensis* var. *dissecta*; R, rootstock cultivars. The numbers just before the lines in the figure represent the accession numbers, which correspond to the same cultivars as in **Table 1**.

Seed extractable resveratrol amounts in rootstock cultivars varied significantly with their genetic backgrounds. The highest seed extractable resveratrol was found in a hybrid obtained from *V. monticula* × *V. riparia*, 'Zhi 168', with 28.56 and 35.06 μg g^{-1} of seed FW in 2003 and 2004, respectively. Another hybrid from *V. monticula* × *V. riparia*, 'Zhi 166', also produced very high resveratrol levels, and these seed extractable amounts reached 23.15 and 23.72 μg g^{-1} of seed FW in 2003 and 2004, respectively. The extractable amounts of resveratrol in seeds of '188-8' (a hybrid from *V. monticula* × *V. riparia*) and '101-14' (a hybrid from *V. riparia* × *V. rupestris*) were also higher, reaching 19.42 and 23.15 μg g^{-1} of seed FW in 2003 and 21.66 and 23.72 μg g^{-1} of seed FW in 2004, respectively. However, extractable amounts of resveratrol in seed of 'ARH2' (a hybrid from *V. amurensis* × *V. riparia*), '5A' (a hybrid from *berlandier* × *V. riparia*), and 'Beta' (a hybrid from *V. riparia* × *V. lubrusca*) were 1.71 and 4.28 μg g^{-1} of seed FW in 2003 (there were no Beta data in 2003) and 0.62, 2.58, and 0.14 μg g^{-1} of seed FW in 2004, respectively.

Similar to extractable amounts of resveratrol in berry skin, the cultivated cultivars, including the winemaking and table grape cultivars of *V. vinifera*, and interspecific hybrid cultivars between *V. labrusca* and *V. vinifera* had much lower extractable resveratrol amounts in seeds than the previous rootstocks.

The extractable amounts of resveratrol in berry seeds of wine grape cultivars of *V. vinifera* ranged from 0.08 to 5.53 μg g^{-1} of seed FW with a median of 0.90 μg g^{-1} of seed FW in 2003 and from 0.01 to 4.16 μg g^{-1} of seed FW with a median of 1.42 μg g^{-1} of seed FW in 2004, respectively. The cultivar 'Wuyuezi' had the highest amounts of extractable resveratrol among wine grape cultivars of *V. vinifera*, and its amount was 5.53 μg g^{-1} of seed FW in 2003 and 4.16 μg g^{-1} of seed FW in 2004. Another five wine grape cultivars of *V. vinifera* with higher amounts of extractable resveratrol were 'Su 162' (3.26 and 2.10 μg g^{-1} of seed FW in 2003 and 2004, respectively), 'Ugni Blanc' (2.91 and 2.37 μg g^{-1} of seed FW in 2003 and 2004, respectively), 'Chardonnay' (2.75 μg g^{-1} of seed FW in 2003), 'Meichun' (1.92 and 1.42 μg g^{-1} of seed FW in 2003 and 2004, respectively), and 'Merlot' (1.04 and 2.09 μg g^{-1} of seed FW in 2003 and 2004, respectively).

The extractable amounts of resveratrol in seeds of table grape cultivars of *V. vinifera* ranged from 0.02 to 2.78 μg g^{-1} of seed FW with a median of 0.99 μg g^{-1} of seed FW in 2003 and from 0.06 to 2.93 μg g^{-1} of seed FW with a median of 1.27 μg g^{-1} of seed FW in 2004. The cultivar 'Fenghuang 51' produced very high amounts of extractable resveratrol in berry seed, reaching 2.30 and 2.19 μg g^{-1} of seed FW in 2003 and 2004, respectively. Another five *V. vinifera* table grape cultivars with relatively high amounts of extractable resveratrol were 'Zaomanao' (2.78 μg g^{-1} of seed FW in 2003), 'Queen of Vineyards' (2.93 μg g^{-1} of seed FW in 2004), 'Huaze Lizamate' (2.22 μg g^{-1} seed FW in 2004), 'Jingxiu' (1.64 and 1.26 μg g^{-1} of seed FW in 2003 and 2004, respectively), and 'Zaoyu' (1.61 and 1.33 μg g^{-1} of seed FW in 2003 and 2004, respectively).

Table grape cultivars of the hybrids between *V. labrusca* and *V. vinifera* had extractable amounts of resveratrol in seeds ranging from 0.15 to 2.98 μg g^{-1} of seed FW with a median of 1.25 μg g^{-1} of seed FW in 2003 and from 0.13 to 2.76 μg g^{-1} of seed FW with a median of 1.33 μg g^{-1} of seed FW in 2004. Two cultivars containing higher amounts of extractable resveratrol were cv. 'Tano Red' and 'Jifeng'. Their extractable amounts of resveratrol in seed were 2.98 and 1.35 μg g^{-1} of seed FW in 2003 and 2004 for 'Tano Red' and 1.92 and 2.02 μg g^{-1} of seed FW in 2003 and 2004 for 'Jifeng', respectively.

In interspecific cultivars for processing use, extractable amounts of resveratrol in seeds were much lower than the median of the winemaking and table grape cultivars of *V. vinifera* and the table grape cultivars of the interspecific hybrids

Table 2. Linearly Independent Pairwise Comparison of Extractable Amounts (Micrograms per Gram of Skin or Seed Fresh Weight) of Resveratrol in Skin and in Seeds between 2003 and 2004

berry organ	genotype group[a]	av extractable resveratrol 2003	av extractable resveratrol 2004	diff between 2004 and 2003
skins	all cultivars studied in both years (70)	6.69	12.25	5.56***[b]
	rootstock cultivars (6)	69.80	130.87	61.07***
	table grape of LV (30)	0.48	0.88	0.41***
	table grape of V (18)	0.55	0.81	0.27***
	wine grape of V (11)	1.15	1.63	0.48***
seeds	all seeded cultivars studied in both years (58)	2.97	3.14	0.17
	rootstock cultivars (6)	17.03	18.65	1.62
	table grape of LV (25)	1.26	1.34	0.08
	table grape of V (11)	1.16	1.19	0.03
	wine grape of V (11)	1.75	1.65	–0.10

[a] LV, hybrids between *V. labrusca* and *V. vinifera*; V, *V. vinifera*. Number in parentheses following the genotype group indicates the number of cultivars used for the analysis. All cultivars used for the analysis in this table had the data in two successive years, represented in detail in **Table 1**. [b] *** indicates significant difference at $P < 0.001$ between 2003 and 2004.

between *V. labrusca* and *V. vinifera*. However, extractable amounts of resveratrol in seeds varied greatly from one genotype to another (**Figure 4**). Extractable amounts in seeds of wine grape cultivars 'Beichun', 'Beihong', and 'Beiquan' were just 0.43, 0.30, and 0.50 μg g^{-1} of seed FW in 2003 and 0.74, 0.94, and 0.42 μg g^{-1} of seed FW in 2004, respectively. The extractable resveratrol amounts in seeds of two juice grape cultivars from *V. thunbergii* × *V. vinifera*, 'Beifeng' and 'Beizi', in 2003 were much higher than that from 'Honey Juice', a hybrid of *V. vinifera* × *V. labrusca* in 2004. The extractable amounts of resveratrol of 0.64 and 0.96 μg g^{-1} of seed FW were observed in the first two, whereas there was only 0.22 μg g^{-1} of seed FW in the latter. The juice grape cultivar 'Russia Concord', a hybrid between *V. amurensis* and *V. lubrusca*, had extractable resveratrol amounts of 0.43 μg g^{-1} of seed FW in 2003 and 0.98 μg g^{-1} of seed FW in 2004.

Similar to extractable resveratrol amounts in berry skin, higher amounts of extractable resveratrol in seeds were found in the Chinese wild species *V. amurensis* var. *dissecta* in both years, reaching 5.00 and 3.69 μg g^{-1} of seed FW in 2003 and 2004, respectively.

Effect of Climate Conditions on Extractable Amounts of Resveratrol. There were significant differences of extractable amounts of resveratrol in berry skin between 2003 and 2004 when the same 70 grape genotypes were studied in two successive years (**Table 2**). The average extractable resveratrol amount in berry skin from all 70 grape genotypes was 12.25 μg g^{-1} of skin FW in 2004, 83% higher than that in 2003. Moreover, the effect of climate conditions on extractable resveratrol amounts in berry skin was higher on the rootstock cultivars and table grape cultivars of hybrids between *V. labrusca* and *V. vinifera* than on the cultivars of *V. vinifera* including table and wine cultivars. In 2004, compared to 2003, average extractable amounts of resveratrol increased 84.9 and 87.4%, respectively, in 6 rootstock grape cultivars and 30 table grape cultivars of hybrids between *V. labrusca* and *V. vinifera*. In cultivars of *V. vinifera*, there was 41.5 and 48.6% more extractable resveratrol in 2004 than obtained in 2003 from 18 table and 11 wine grape cultivars, respectively. However, the effect of climate on the extractable resveratrol amounts in seeds was negligible, and there were no significant differences in extractable resveratrol in seeds between 2003 and 2004 for all grape genotype groups.

Relationships of Skin and Seed Extractable Resveratrol Amounts and the Different Fruit Traits or Purpose of Uses. **Table 3** shows the average extractable resveratrol amounts in berry skin and seeds in 2003 and 2004 separately, based on different genotype groups, fruit traits (seeded or seedless; red or green), and purpose of uses (table grapes or wine grapes).

The extractable amounts of resveratrol in berries largely depended upon the genetic background of the grapes. The interspecific cultivars used for rootstocks had significantly higher amounts of extractable resveratrol in skins and in seeds than cultivated cultivars of *V. vinifera* and hybrids between *V. labrusca* and *V. vinifera*. The average amounts of extractable resveratrol in skins and seeds of all interspecific cultivars used for rootstocks were 69.80 and 17.03 μg g^{-1} of seed FW in 2003 and 145.11 and 16.07 μg g^{-1} of seed FW in 2004, whereas those of cultivated cultivars of *V. vinifera* and hybrids between *V. labrusca* and *V. vinifera* were 0.61 and 1.30 μg g^{-1} of seed FW in 2003 and 1.24 and 1.36 μg g^{-1} of seed FW in 2004, respectively.

The extractable resveratrol amounts also depended upon the genotype groups for the cultivated cultivars. The cultivated cultivars of *V. vinifera* had significantly higher amounts of extractable resveratrol in berry skin than did hybrids between *V. labrusca* and *V. vinifera* in both years. However, there were no significant differences in the amounts of extractable resveratrol in seeds between cultivars of *V. vinifera* and those of hybrids between *V. labrusca* and *V. vinifera*.

For all seeded cultivars of *V. vinifera* and the hybrid cultivars of *V. labrusca* × *V. vinifera* in this study, the extractable amounts of resveratrol in seeds were double that and significantly higher than that in berry skin in 2003. However, there were no significant differences in extractable resveratrol amounts in seeds and skin in 2004. In addition, seeded cultivars had significantly higher amounts of extractable resveratrol in skin, almost double that in seedless cultivars in 2004, although in 2003 there were no significant differences between seeded and seedless cultivars in extractable resveratrol amounts in berry skin.

Red-berry cultivars (including all red, purple, and black cultivars) had significantly higher amounts of extractable resveratrol in skin and seeds than green-berry cultivars (including all green, yello2, and white cultivars) in both years. The amounts of extractable resveratrol from the former were 50−96.6% higher in skin (0.66 and 1.44 μg g^{-1} of skin FW in 2003 and 2004, respectively) and 10.2−13.1% higher in seeds (1.34 and 1.40 μg g^{-1} of seed FW in 2003 and 2004, respectively) than the latter (0.44 and 0.73 μg g^{-1} of skin FW and 1.22 and 1.23 μg g^{-1} of seed FW in 2003 and 2004, respectively).

With regard to purpose of uses, winemaking cultivars originating from *V. vinifera* had significantly higher resveratrol in both skins and seeds than table grape cultivars from *V. vinifera* in both years.

DISCUSSION

The results obtained from the study during two successive years of 120 grape cultivars showed that there was a great variation in the amounts of extractable resveratrol in berry skin and seeds within and among different grape genotype groups, indicating that both skin and seed resveratrol synthesis depended largely upon grape genetic background. All three rootstock cultivars obtained from hybrids of *V. monticula* × *V. riparia*,

Table 3. Comparison of Extractable Amounts of Resveratrol in Skin (Micrograms per Gram of Skin Fresh Weight) and in Seeds (Micrograms per Gram of Seed Fresh Weight) among Different Grape Genotype Groups or Purpose of Uses

	av extractable resveratrol in 2003		avg extractable resveratrol in 2004	
genotype group or purpose of use[a]	skin	seed	skin	seed
all cultivated cultivars of V and LV	0.61	1.30	1.24	1.36
all rootstocks of interspecies	69.80***[b]	17.03***	145.11***	16.01***
all seeded cultivars of LV and V	0.61B[c]	1.37A	1.33***	1.36
all seedless cultivars of LV and V	0.59		0.85	
all red-berry cultivars of LV and V	0.66***	1.34*	1.44***	1.40***
all green-berry cultivars of LV and V	0.44	1.22	0.73	1.23
all cultivars of LV	0.41	1.35	0.88	1.37
all cultivars of V	0.81***	1.239	1.604***	1.341
V. vinifera wine grapes	1.03***	1.43***	2.50***	1.43***
V. vinifera table grapes	0.67	1.06	1.02	1.25

[a] LV, hybrids between *V. labrusca* and *V. vinifera*; V, *V. vinifera*. [b] * and *** indicate significant difference in the same berry organ (skin or seeds) in the same year between different genotype groups or purpose of uses at $P < 0.05$ and $P < 0.001$ levels, respectively. [c] Means followed by the different capital letters indicate significant difference between berry skin and seeds in the same year at $P < 0.001$ level.

especially 'Zhi 166' and 'Zhi 168', had extremely high amounts of extractable resveratrol in the berry skin and seeds and their the extractable resveratrol amounts were >100 μg g^{-1} of skin FW and >20 μg g^{-1} of seed FW (**Figures 3** and **4**). The amounts of extractable resveratrol from berries of rootstock cultivars that are descendants of *V. riparia* were also high. 'Beta', a hybrid from *V. labrusca* × *V. riparia*, had 230.52 μg g^{-1} of skin FW of extractable resveratrol in 2004, and '101-14', a hybrid from *V. riparia* × *V. rupestris*, had 32.21−59.29 μg g^{-1} of skin FW and 23.15−23.72 μg g^{-1} of seed FW. The lowest amounts of extractable resveratrol among rootstock cultivars related to *V. riparia*, 'ARH2', a hybrid from *V. amurensis* × *V. riparia*, and '5A', a hybrid from *V. berlandier* × *V. riparia*, ranged from 7.90 to 20.12 μg g^{-1} of skin FW, and those amounts were much higher than in those interspecific hybrids unrelated to *V. riparia*, such as hybrids between *V. labrusca* and *V. vinifera* (cvs. 'Venus' and 'Takasuma'), hybrids from *V. vinifera* × *V. amurensis* (cvs. 'Beichun', 'Beihong'. and 'Beiquan'), and hybrids from *V. thunbergii* × *V. vinifera* (cvs. 'Beizi' and 'Beifeng'). Our results suggest that *V. riparia* should have genes for high levels of resveratrol synthesis as should descendents of *V. riparia*.

The genus *Vitis* includes two subgenera, *Muscadinia* Planch. and *Euvitis* Planch. High amounts of extractable resveratrol have been found in muscadine grapes, *V. rotundifolia*, in the subgenus *Muscadinia*, for which extractable resevratrol amounts of about 44 μg g^{-1} of seed FW were found (*7*). Here, all of the materials used were *Euvitis* genotypes, and we now know that there are genotypes rich in resveratrol in this subgenus. However, we also know that *Euvitis* consists of more than 70 species, most of which are wild, and studies on resveratrol have been carried out only on a small number of these species, for example, *V. vinifera* and *V. labrusca* grapes (*6*, *8*), and some species and interspecfic hybrids. With this lack of information on resveratrol in so many species of *Vitis*, it is important to investigate the resveratrol resource, especially in wild species, to use directly the natural resveratrol resource for human consumption or indirectly in breeding programs to obtain new grape cultivars with high amounts of extractable resveratrol in their berries.

Compared to the wild species *V. amurensis* var. *dissecta* and the other interspecific hybrids, cultivars of the European type (*V. vinifera*) and hybrids with *V. labrusca* had relatively low amounts of extractable resveratrol in the berry. With a few exceptions, the extractable amounts of resveratrol in berry skins and seeds were <2 μg g^{-1} of skin or seed FW. These great variations in extractable resveratrol amounts in *Vitis* show an important potential for exploiting high resveratrol grape germplasms for developing grape cultivars with high levels of resveratrol for different uses, such as grapes for fresh market, wine, and juice. However, there are also great variations within the same species and the same type (**Figures 3** and **4**). The berry skin of some cultivated cultivars, such as 'Jingzijing', 'Superior Seedless', 'Fenniu', and 'Muscat Hamburg', had much higher amounts of extractable resveratrol than the other table grape cultivars, and 'Cabernet Gernischet', 'Merlot', and 'Wuyuezi' had higher amounts than the other winemaking cultivars within *V. vinifera*.

Most table grape cultivars in Asia, especially in China and Japan, are hybrids between *V. labrusca* and *V. vinifera* rather than cultivars of *V. vinifera*. Higher sugar contents, as well as a low ratios of glucose/fructose, in the former than in the latter explain why Asian farmers prefer to plant table grape cultivars of hybrids between *V. labrusca* and *V. vinifera* (*19*). Asian people prefer to consume sweet fruits, especially those with a higher ratio of soluble solids/total acids. Moreover, Asian people do not like berry skin and seeds and discard these when eating grapes. However, this study shows that berry skin and seeds were often rich in resveratrol (**Figures 3** and **4**), and the interspecific hybrid cultivars between *V. labrusca* and *V. vinifera* had lower resveratrol contents than *V. vinifera* cultivars (**Table 2**). It could be beneficial to grow more *V. vinifera* cultivars and convince Asian people to consume more *V. vinifera* grapes with skin and seeds together with flesh to increase dietary sources of resveratrol.

The extractable amounts of resveratrol in berry depend largely on the genetic background, as discussed above. However, resveratrol is a phytoalexin, and its synthesis can be activated by exogenous stress factors, such as injury, ultraviolet irradiation, and pathogenic fungi (*20*). The climate in the summer of 2004 differed greatly from that in 2003 in Beijing. The summer of 2004 was characterized by greater and more frequent rainfall with a high relative humidity as compared to 2003 (**Table 4**). Moreover, there were fewer sunshine hours during August and more sunshine hours during July and September in 2004 than in 2003. Sunshine hours affected ultraviolet irradiation arriving on the earth's surface in nature. Ultraviolet radiation can be divided into three parts according to wavelength: ultraviolet A (320−400 nm), ultraviolet B (280−320 nm), and ultraviolet C (<280 nm). Ultraviolet radiation is reduced when it passes through the ozonosphere, and ultraviolet absorption differs depending on the wavelength. Ozone absorbs very little ultraviolet A, but most ultraviolet B, and ultraviolet C is completely absorbed by stratospheric ozone and does not reach the earth surface. Only ultraviolet C stimulates resveratrol

Table 4. Climate Conditions in Summer during 2003 and 2004

	mean temperature (°C)			relative humidity (%)			rainfall (mm)			sunshine (h)		
year	July	Aug	Sept	July	Aug	Sept	July	Aug	Sept	July	Aug	Sept
2003	25.2	25.5	19.8	66	61	69	65.5	30.5	104.4	171.0	245.9	174.8
2004	25	23.8	20.2	68	68	59	173	132	55.6	220.0	202.5	213.7

synthesis tremendously (*21*), so sunlight is not an important factor stimulating resveratrol synthesis under field conditions. The differences in the extractable amounts of resveratrol between 2003 and 2004 observed in this study (**Table 2**) may have been caused by other climate factors. We know that the fungal diseases in grape, such as downy mildew [*Plasmopara viticola* (Berk. et Curt) Berl. et De Toni] and powdery mildew [*Uncinula necator* (Schw.) Bur.], vary with climate, and rainfall and humidity during the growing season are more favorable to fungi than a dry year. More severe diseases were found in the vineyard in 2004 than in 2003. Significantly higher amounts of resveratrol were synthesized in the skin of berry in 2004 than in 2003, whereas there were no significant differences in resveratrol in seeds between the two years (**Table 2**). Resveratrol synthesis may have been a response to disease resulting from high relative humidity or great rainfall, but only in berry skin, not in seeds. This difference in the response of resveratrol synthesis suggests that the synthesis and accumulation of resveratrol in grape berry skin should be more sensitive to climate change than seeds and that resveratrol should be synthesized independently in seed and skin tissues, with little exchange between these tissues.

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