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Ethylene and grape berry ripening

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Abstract

Purpose of the review: The involvement of ethylene in fruit ripening has been the subject of intensive molecular and biochemical studies over the last twenty years. Whereas new methods and new genes are being discovered, the differences between climacteric and non-climacteric fruit seem to decrease. Recent studies are showing potential roles for ethylene signals in grape berry ripening.

Main findings: Ethylene seems to be involved in some changes that occur during the grape berry ripening, the final step of berry development. The whole ethylene production pathway seems activated at the inception of the grape berry ripening, the veraison. Treatments with exogenous ethylene stimulate the long term expression of genes related to the anthocyanin synthesis. Ethylene signals are also involved in the regulation of vascular fluxes and acid content. The ethylene may also been involved in some steps of aroma production, modulated by alcohol dehydrogenases.

Directions for future research: These findings could help to further unravel the differences between climacteric and non-climacteric fruit. In the future, whole genome sequencing and computer analyses will surely provide new tools to complete our knowledge of ethylene involvement in the ripening of these two categories of fruit. Regarding the economic importance of fruit ripening and preservation, this knowledge is crucial.

Keywords: ethylene, grape, *Vitis vinifera*, climacteric, signalling, anthocyanin, vascular flux, acidity, methylcyclopropene

Abbreviations

ACC	1-aminocyclopropane-1-carboxylic acid
ACO	ACC oxidase
ACS	ACC synthase
ETR1	ethylene receptor 1
ETR2	ethylene receptor 2
EIN4	ethylene insensitive 4 (receptor)
ERS1	ethylene response Sensor 1 (receptor)

ERS2	ethylene response sensor 2 (receptor)
CTR1	constitutive triple response 1 (ethylene receptor ‘central unit’)
1-MCP	1-methylcyclopropene
2-CEPA	2-chloroethylphosphonic acid (also named “ethephon”)
UFGT	UDP glucose-flavonoid glycosyltransferase
ADH	alcohol dehydrogenase

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Introduction

Ethylene in plant biology

Ethylene is a gaseous compound (C₂H₄) which has wide-ranging functions in plant biology [1]. Firstly, ethylene is involved in most development steps of the plant life cycle, including seed germination, root hair development, root nodulation, flowering, fruit ripening, abscission and senescence [1, 2**, 3]. Secondly, it could be considered as a “stress hormone”, because it possesses a determinant role in responses to environmental stimuli from biotic (pathogen attack) and abiotic stresses, such as wounding, hypoxia, ozone, chilling or freezing [2**].

What is ripening?

Fruit development and ripening are two steps that are plant specific, and render the fruit attractive to a variety of seed-dispersing organisms [4, 5**]. Ripening, like the senescence that follows, are genetically programmed steps of plant development which can be modulated by internal (hormones) or external (light, humidity, temperature) signals [5**]. Thus, the mature phenotype results from number of physiological and biological variations, like colour change due to pigment modification, softening and flavour elaboration with sugar and volatile compound accumulation [3, 6**, 7].

Classification of climacteric or non-climacteric fruit

Concerning the ripening phase, fruit is classified into two categories: climacteric and non-climacteric. The first category includes pear, apple, kiwi, banana, peach, apricot, melon and tomato; the second one includes pineapple, cherry, fig, strawberry, citrus fruits and grape, among others [3]. Climacteric fruit ripening is associated to important rises in respiration and ethylene synthesis, on the contrary to non-climacteric fruit ripening [3]. Since this

classification, new observations have described complex interactions in the ethylene pathways (biosynthesis and perception), their implications in fruit ripening, and particularly in grapes, which is the subject of this review.

Known roles for ethylene in fruit ripening

Over the last twenty years, the biochemistry of ethylene biosynthesis has been a subject of intensive studies. Today, the major steps of the production pathway have been discovered [2**]. Additionally, the molecular cloning of the ACS and the ACO genes has now been performed in many plant species [2**, 7] and have led us to understand their regulation by a complex network of developmental and environmental signals responding to both internal and external stimuli [2**].

Recently, Brummell [7] reviewed the two distinctive biosynthesis systems. System 1 corresponds to the immature fruit development implying a weak ethylene synthesis, and to non-climacteric behaviour throughout all fruit development stages. System 2 refers to the massive production of this hormone in response to its own stimulation, named “autocatalytic synthesis”, specific to climacteric fruit. Most enzymes of the ethylene production, and probably perception, are involved. However, the transition between the two systems is not well understood, none specific molecular candidate of these two systems being isolated, and this could represents a new way for future research [7, 8]. The ethylene signal transduction pathway was first elucidated using the *Arabidopsis thaliana* model [1]. Then, these findings were verified in tomato, a fleshy fruit model [9] and checked in strawberry, non-climacteric fruit [10]. In *A. thaliana*, there are five known ethylene receptors (ETR1, ETR2, EIN4, ERS1 and ERS2) [11, 12] and six homologues were found in tomato, LeETR [9]. When ethylene is not bound to them, the receptors could be considered like negative regulators of the hormone signal, because they constitutively “activate” CTR1 in *A. thaliana*, and three CTR1 homologues in tomato [5**], which in turn, negatively regulate the downstream signal pathway through a MAP-kinase cascade [1, 2**, 5**, 6]. MAP stands for Mitogen-Activated Protein.

A quite recent tool, 1-methylcyclopropene (1-MCP), an inhibitor of ethylene action, was discovered by E. Sisler and colleagues. Blankenship and Dole [13*] wrote a comprehensive review about it. 1-MCP is a gas under ambient conditions and is thought to irreversibly bind ethylene receptors with an affinity ten times greater than that of ethylene [13*]. In the presence of 1-MCP, CTR1 maintains a signal inhibition configuration in the transduction pathway [8].

1 Today, the development of grape genome sequencing provides new tools to find putative
2 orthologues to *A. thaliana* genes, involved in this pathway [5**, 6]. Thus all these genes
3 could represent as many clues to extend our knowledge about ethylene signalisation in this
4 non-climacteric fruit [5**, 6]. Recently, Hilt and Bessis [14] reported a relation between the
5 ethylene biosynthesis and the abscission of fruitlets during grape bloom. Therefore, this
6 observation confirms the possibility that ethylene plays a role in other life cycle steps. And
7 what about its role in grape ripening?

10 **What is known about grape ripening?**

12 In grape, ripening represents the second phase of berry development. The grape berry exhibits
13 a double sigmoid pattern of growth with two distinct phases separated by a lag phase [15*,
14 16*, 17*]. The first phase begins with a burst of cell division in pericarp tissue, which
15 determines the berry final shape [15*, 16*]. The water for the volume expansion derives from
16 both xylem and phloem sap, but more specifically from xylem. The main solutes to
17 accumulate are the acids, particularly tartaric and malic [15*, 17*]. The second phase of grape
18 berry development corresponds to the ripening. It results from the expansion of existing
19 pericarp cells. A number of major physiological and biochemical simultaneous changes is
20 characteristic to this ripening phase and determines the quality of the fruit at harvest [15*,
21 16*]. Significant changes in metabolism begin at “véraison”, the onset of ripening, including
22 sugar accumulation in flesh and skins, softening of berries, synthesis of anthocyanins and
23 accumulation in skin, catabolism of organic acids and accumulation of flavour compounds
24 [15*, 16*]. Concerning the vascular fluxes, the xylem flow is strongly reduced, hence the
25 water and sugar that move during this phase largely come from phloem sap [15*, 17*]. At the
26 inception of ripening, before the second phase of berry growth, Coombe and Hale [18*] did
27 not observe an ethylene burst as in climacteric fruit, but Alleweldt and Koch did [19*].

28 Beside these variations in ethylene content that are rather small, we observed that the whole
29 ethylene synthesis pathway was activated, and that the major component that accumulated
30 was the malonylated ACC form [20*].

31 As a spin-off of these studies, we checked the effects of ethanol in modulating grape ripening.
32 Indeed in tomato, Beaulieu and Saltveit [21*] observed that a treatment with ethanol
33 accelerated ripening and stimulated ethylene synthesis. Chervin and al. [22] observed a
34 similar stimulation after spraying grape clusters with ethanol (5 % in water, hand-sprayer and
35 saturation of the berry surface).

Ethylene and grape berry colour

Many authors have showed that grapevine treatments with ethylene precursors stimulate the berry coloration. The 2-chloroethylphosphonic acid (2-CEPA), around 500 to 1000 mg/litre, was tested on grapevine by Hale and al. [23*]. This compound is also named ethephon. It enhanced ripening, with an associated increase of the number of coloured berries per cluster. Its application has been shown to increase anthocyanin synthesis in “Ruby Cabernet” and “Zinfandel” grapes [24]. This has been confirmed by other studies, among which one report by Shulman and al. [25], where the authors showed that ethephon improved maturation and wine quality of “Carignane” grapes, in a warm region of Israel. These results have led to the commercial development of ethephon solutions. We have observed recently that such solutions can advance maturity of “Cabernet Sauvignon” in the foothills of the Pyrenean chain, a cool climate place in the South West of France (Chervin C., pers. comm.). The application of ethylene precursors, such as ethephon, was demonstrated to stimulate the long term expression of genes related to anthocyanins synthesis [26], more than 10 to 20 days after treatment. This may be linked to a sustained ethylene evolution from treated berries previously observed by Coombe and Hale [18*]. This sustained production of ethylene seems to reach higher quantities than those being applied as precursors, and suggests that there is some feedback in the grape tissues, even if the ethylene evolution does not evolve in a massive increase as in climacteric fruit [3]. The ethylene stimulation of the expression of anthocyanin synthesis genes was linked to an increased accumulation of all the major anthocyanins without a change towards a specific type of anthocyanin accumulation [26]. The important role of ethylene in anthocyanin accumulation in berry skin tissues was confirmed by the inhibition of anthocyanin accumulation, induced by gassing the clusters with 1-MCP at veraison; this was performed by applying 1-MCP in a bag surrounding the cluster [20*].

As we showed that ethanol stimulates ethylene evolution by the grape clusters [22], we tested the ethanol effect on the expression of some anthocyanin biosynthesis genes [27], and found that one was increased by this alcohol, the UDP glucose-flavonoid glycosyltransferase (UFGT). This is sought to be a key step in anthocyanin accumulation in plant tissues as the glycosylation stabilises the anthocyanin. We have since sequenced more than 1500 base pairs of the UFGT promoter (GenBank accession number AY955269) and observed that it contains several ethylene cis-elements. This gene is also thought to be strongly regulated by a Myb transcription factor [28]. Whether this factor depends on ethylene signals or not, is unknown.

Ethylene and vascular fluxes in grape berry

Gassing clusters with 1-MCP limits the increase of berry volume during the ripening phase [20*]. The effect of 1-MCP was particularly important at the inception of ripening when there was a concomitant rise in ethylene evolution and associated biosynthesis pathway. During the following ripening period, the volume extension of the berry is thought to be mainly due to phloem fluxes [15*, 16*, 17*]. The observation that 1-MCP limits the increase of the berry diameter is a first proof of potential roles for ethylene signals in regulating the vascular fluxes associated to berry ripening.

When regarding the effects of spraying ethanol onto clusters, we observed an increased berry size in France and Australia, in quite different conditions [29]. This is logical compared to the results obtained with 1-MCP, if we consider that ethanol slightly stimulates the endogenous ethylene production; this confirms that ethylene could boost vascular fluxes. However, it is known by industry people that massive doses of ethephon can lead to a decreased berry size.

Ethylene and grape acidity

Ethylene seems also implicated in the regulation of berry acidity. Indeed, ethephon treatment induces an acidity decrease in grape juice [25]. These authors observed the acidity drop in musts and wines of “Carignane” grapes over two seasons, and this was linked to the concentration decrease of both tartaric and malic acids. We recently confirmed these observations in a cool climate region on “Cabernet Sauvignon” (Chervin, unpublished). We also observed that gassing clusters with 1-MCP led to a slower decrease of acidity over the ripening phase [20*]. As the acidity was measured in equivalent per litre of juice, we cannot conclude whether this effect was directly related to ethylene signalling or indirectly related reflecting the smaller diameter of treated berries, thus leading to less juice per berry, which in turns leads to a smaller dilution of the same quantity of acids.

As the acidity was measured in equivalent per litre of juice, we cannot conclude whether this effect was directly related to blocked ethylene signals limiting acid degradation, or indirectly related, reflecting the smaller diameter of treated berries, leading to less juice per berry and a smaller dilution of the same quantity of acids.

This is somehow controversial with known effects of ethephon leading globally to smaller berries with lower acidity, compared to controls.

1 And finally regarding berry acidity, we observed a decreased acidity by spraying ethanol onto
2 the “Cabernet Sauvignon” clusters [30]; the malic acid was the only acid affected in this case.

5 **Ethylene and aroma in grape berries and wine**

7 Not much is known about the ethylene role in grape flavour and aroma. Ethylene stimulates
8 one specific *Vitis vinifera* alcohol dehydrogenase (VvADH) implicated in the grape ripening
9 phase [31*]. In plants, the ADHs have a variety of functions: detoxification, stress response,
10 aldehyde/alcohol ratio regulation. This last reaction may have some potential in changing the
11 aroma production as stated by other authors working with tomato [32]. Tesnière and al.
12 showed the presence in the VvADH promoter of cis-elements for ethylene, suggesting that the
13 ethylene transduction pathway could be partly involved in the regulation of the expression of
14 this enzyme [31*].

15 The fact that lots of aroma precursors are glycosylated [15*] is another track to follow in the
16 search for hormonal regulation of these critical steps for berry quality gain. At present, Boss
17 and colleagues are working to decrypt the complex mechanisms of aroma formation in grapes.

20 **Perspectives**

22 Since the 70's, the grape has been classified as a non-climacteric fruit [3]. This does not mean
23 that ethylene has nothing to do with grape and other non-climacteric fruit ripening. Recent
24 data confirm this. An autocatalytic system 2-like ethylene synthesis was observed in citrus in
25 response to initial low amounts of this hormone. This rise in ethylene production is preceded
26 by induction of the genes for CsACS1 and CsACO1 and one of the receptors, CsERS1 [33*].
27 Other results have been obtained recently in strawberry, another non-climacteric fruit, in
28 which two cDNAs coding for enzymes of the ethylene biosynthesis pathway (FaACO1 and
29 FaACO2) and three cDNAs encoding different ethylene receptors (FaETR1, FaETR2 and
30 FaERS1) have been isolated [34*]. These observations suggest perhaps a similar way of
31 ethylene signalisation in climacteric and non-climacteric fruits. The only distinction could be
32 based on the sensitivity of the hormone receptors, or the ethylene rate required to induce the
33 response, or some missing link to trigger the autocatalytic rise in some non-climacteric fruit.
34 Perhaps, new methods like whole genome sequencing and computer analyses will permit to
35 elucidate the ethylene involvement in grape berry ripening, and to measure the real
36 differences between climacteric and non-climacteric fruits. The recent development of grape

1 microarray has revealed the first large pool of genes involved in the inception of grape berry
2 ripening [35]. Other plant hormones that are involved in grape ripening are under scrutiny of
3 research groups at the moment: brassinosteroids [36] and jasmonates [37], and these may
4 have interactions with ethylene signalling.

5 Among these critical works, some potential for ethanol applications have derived from works
6 on the relations between ethylene and ethanol. Indeed the table grape preservation is
7 improved in presence of ethanol vapours [29].

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