

Aroma Development during Ripening of *Fragaria chiloensis* Fruit and Participation of an Alcohol Acyltransferase (FcAAT1) Gene

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Fragaria chiloensis is characterized for having great aroma and flavor properties. Using headspace-SPME different volatile compounds were identified and quantified during development and ripening of the fruit. The headspace was dominated by esters, butyl acetate, ethyl acetate, ethyl butanoate and ethyl hexanoate being the most abundant in fully ripe fruit. As esters are important for aroma and synthesized through alcohol acyltransferases (AAT), a full-length cDNA (*FcAAT1*) was isolated from *F. chiloensis* fruit which displayed the three motifs characteristic of most AATs. As the production of esters increased during ripening, a clear increment in *FcAAT1* transcripts was observed in fruit tissue. A good correlation was found between AAT activity and the total content of esters, especially with acetates and hexanoates. Aroma-related esters displayed during ripening the same production profile as AAT activity. Therefore it can be suggested that the *FcAAT1* gene may have a significant role in ester production of *F. chiloensis* fruit.

KEYWORDS: Alcohol acyltransferase; aroma; esters; *Fragaria chiloensis*; fruit ripening; Chilean strawberry

INTRODUCTION

Fragaria chiloensis L. (Duch.), the native Chilean strawberry, is considered to have potential to become a new exotic fruit species that could add to the diversity of berry fruits that Chile can export. Although populations of F. chiloensis have been used since 1000 years ago by the indigenous "Mapuches" in the central-south part of Chile (1), with the introduction of modern commercial cultivars of strawberry (Fragaria × ananassa Duch.) the improvement of F. chiloensis was not continued. Nowadays, $F. \times$ ananassa is the strawberry species grown worldwide, developed after the fortuitous cross of two wild octoploid species, Fragaria virginiana Duch. and F. chiloensis (1). F. chiloensis, the mother of the commercial strawberry, is characterized for having great aroma and flavor properties, a remarkable pest and disease resistance spectrum, resistance to salinity and drought and low nutrient needs, along with other characteristics that make it an attractive species for plant research (2). Indeed, research on this species has been focused on its development as a new exotic berry fruit, as well as for the genetic improvement of $F. \times ananassa(2)$.

Among the many quality parameters defining the desirability of fruit and vegetables, there are important nonvisual characteristics which influence the final acceptance by consumers, such as texture, nutritional value, flavor and aroma (3). In strawberry, appearance (color, size, form, absence of damage), firmness, flavor (solid soluble, titratable acidity, aromatic compounds) and nutritional value (vitamins and antioxidant content) define fruit quality (4). Aroma is an important trait to consider in a strawberry breeding program if the goal is to improve fruit quality. Fruit aroma is determined by a large number of volatile compounds, and their production is dependent on many factors, such as cultivar, maturity, and storage conditions (5). The molecular mechanism by which fruit flavor and aroma compounds are gained and lost during evolution and domestication are largely unknown.

Commercial strawberries produce numerous volatile compounds including esters, aldehydes, ketones, alcohols, terpenes, furanones, and sulfur compounds (6, 7). Esters are quantitatively and qualitatively the most abundant class of compounds, comprising from 25% to 90% of the total volatiles in fresh ripe fruit (8). Esters provide the fruity and floral notes of fresh ripe fruit while the sweet fragrance is determined by furanones (9-11). Among the hundreds of volatile compounds produced by a strawberry fruit, only a small portion contribute to its aroma and flavor (5). Compounds like ethyl butanoate, Furaneol and ethyl hexanoate contribute importantly to the aroma of $F. \times$ ananassa fruit, in addition to methyl butanoate, linalool, 2-heptanone and 2-methyl butanoate (12). To date, there is scarce information regarding the aroma compounds produced by F. chiloensis fruit (13).

Volatile content increases rapidly as commercial strawberry fruit ripens (8, 14, 15). There are differences in the production of

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volatiles among strawberry cultivars, both quantitative and qualitative; although the chemical composition of volatiles is dominated by methyl and ethyl esters, the abundance of each ester varied within cultivars (5). On the other hand, diverse aroma patterns are observed between cultivated and wild type species, the wild species being those with the highest concentration of volatiles and better aroma properties, therefore the flavor quality also differs significantly between them (*16*). Reports indicate that the aroma profile of *F. chiloensis* fruit differs from that of *F. × ananassa* (*13*).

Esters are generated by esterification reactions between alcohols and acyl-CoAs, derived from both fatty acid and amino acid metabolism, in a reaction catalyzed by the enzyme alcohol acyltransferase (AAT; EC 2.3.1.84) (17, 18). AATs from strawberry fruit have been characterized at the biochemical and molecular level, and differences in substrate specificity between different genotypes have been demonstrated (19-22). There is an increase in AAT activity along the ripening of strawberry fruit (20). Cultivars with high AAT activity resulted in higher ester production and subsequently in fruits with enhanced aroma (20). In general terms, breeding programs have historically focused on yield, fruit size, shape, shelf life characteristics and disease resistance, having unintended negative consequences on strawberry flavor and aroma (6). Nevertheless, postharvest characteristics, like flavor and aroma, are nowadays taken into consideration in breeding programs; however, as flavor is a complex and multigenic trait, it provides a unique challenge to breeders.

In this work, we report the profile of volatile compounds of *F. chiloensis* fruit and their evolution during fruit development and ripening. Emphasis was placed on ester biosynthesis, considering that these are key aroma compounds. An AAT gene was isolated (*FcAAT1*) and characterized; its expression was analyzed and discussed in relation to the production of esters by the fruit. As far as we know this is the first report that establishes a relationship between ester formation and AAT gene expression during ripening of the Chilean strawberry fruit.

MATERIALS AND METHODS

Plant Material. Chilean strawberries (*F. chiloensis* spp. *chiloensis*) were cultivated in a commercial field located at Contulmo, Biobío Region, Chile (latitude 38° 04' 8.6'' S; longitude 73° 14.2' 96'' W). The plants correspond to the Contulmo accession of *F. chiloensis* and represented macro propagated material done by farmers. *F. chiloensis* fruit from different plants were harvested on the 10th of January 2008 and transported immediately to the University of Talca. Uniform fruit and without defects was classified into four ripening stages according to Figueroa et al. (23): C1, small fruit with green receptacle and green achenes; C2, large fruit with green receptacle and red achenes; C3, turning stage, white receptacle and red achenes; and C4, ripe fruit with pink receptacle and red achenes. Three replicates for each ripening stage were employed on quality assessments. Other plant tissues were collected from the same plants (runners, leaves, flowers and stems), which were frozen under liquid nitrogen and stored at -80 °C until use.

Sampling and Analysis of Volatile Compounds by Headspace-SPME. Fruit from each ripening stage was analyzed for weight, length and diameter. Three replicates of approximately 30 g each (4 intact fruits for C1 stage; 3 for stage C2; and 2 for C3 and C4 stages) were employed for volatile analysis. Each replicate was introduced into a tightly closed container (400 mL) fitted with a rubber septum and incubated at 20 °C for 2 h prior to SPME (solid phase microextraction) sampling. An SPME portable field sampler of $65 \,\mu$ m film thickness of polydimethylsiloxane/divinylbenzene (PDMS/DVB) on a Stableflex fiber (Supelco, USA) was inserted into the chamber through the septum, and exposed to the headspace for 30 min. Volatile compounds adsorbed by partition on the SPME fiber were thermally desorbed in the injector port of the GC at 220 °C (split ratio 6.4). A Perkin-Elmer Clarus 500 gas chromatograph equipped with a SPB-5 capillary column (Supelco, 30 m × 0.25 mm i.d., 0.25 μ m film thickness) and a flame ionization detector (FID) was used (24). Injector and detector temperatures were 200 and 250 °C, respectively. The oven temperature was held at 50 °C for 2 min, and then raised to 220 at 10 °C min⁻¹ and held for 2 min, using helium as a carrier gas (50.3 cm s⁻¹). Quantification of compounds was based on GC-FID peak integration data and by constructing calibration curves with standards under our experimental conditions, from which response factors were obtained. Known amounts of 1,2-dichlorobenzene (0.5 μ L) were added to the chambers as internal standard to check the adsorption capacity of each fiber, and results were expressed as pg g FW⁻¹.

GC–MS analyses were performed on a Perkin-Elmer Autosystem XL/ Turbo Mass 4.1 gas chromatograph, fitted with a MDN-5 column (Supelco, 30 m × 0.25 mm i.d., 0.25 μ m film thickness) (24). Temperature programming was the same as for GC-FID chromatogram; injector temperature was 200 °C; transfer line, 300 °C; and helium as carrier gas (40.2 cm s⁻¹). Mass spectra were obtained by electron ionization at 70 eV with a spectral range of 40–250 m/z. Compound identification was carried out by matching their mass spectra with those of reference compounds stored under the NIST mass spectra library, and whenever it was possible MS identifications were confirmed by comparing their retention times (t_R) with authentic reference compounds obtained from Sigma, Aldrich or Fluka. A linear retention index (LRI) was calculated for each compound using the retention times of a homologous series of C9–C22 *n*-alkanes analyzed under the same conditions.

Fruit Quality Assessment. Firmness was measured using the Firm Tech II (BioWorks Inc., USA) provided with a flat tip of 2 cm. Two measurements on each equatorial side were performed on each fruit. The mean of each replicate (18 fruits per stage) was recorded and expressed as newtons (N) \pm standard error (SE).

After firmness measurement the peduncle and calyx of each fruit were removed, and the fruit was cut into pieces, frozen under liquid nitrogen and stored at -80 °C until use. Two grams of fruit tissue from each replicate was homogenized in water in a Waring blender and adjusted to 25 mL final volume. The mixture was filtrated through miracloth, and the juice was analyzed for soluble solids concentration (SSC), pH, and titratable acidity (TA). SSC was determined at 20 °C using a hand-held temperature compensated refractometer (Atago Co., Tokyo, Japan), and expressed as g g⁻¹ of fresh weight. The pH of the juice was recorded with a pH meter (Pasco Scientific, PS-2117). TA was determined by titration of an aliquot of 5 mL of strawberry juice with 20 mM NaOH until reaching pH 8.2 and expressed as mequiv of citric acid g FW⁻¹.

Assay of AAT Activity. Frozen fruit tissue (10 g) was homogenized in a mortar with the help of liquid nitrogen in the presence of 0.2 g of PVPP and 20 mL of 0.1 M Tris-HCl buffer (pH 8) containing 1 M KCl, 0.1%(v/v) Triton X-100. The mixture was stirred for 20 min at 4 °C, filtrated through miracloth and centrifuged (11000g for 20 min). The supernatant was desalted through a Sephadex G-25 gel filtration column (PD-10 Pharmacia) in the presence of buffer 50 mM Tris-HCl (pH 7.5) containing 10% (v/v) glycerol and 0.5 mM DTT.

AAT activity was quantified by its ability to convert butanol and acetyl-CoA into butyl acetate (25). The reaction was performed in 500 μ L total volume in the presence of 10 mM butanol, 490 µM acetyl-CoA, 50 mM Tris-HCl (pH 7.5) buffer containing 10% (v/v) glycerol. The reaction was initiated by the addition of 300 μ L of protein extract and the mixture incubated at 30 °C for 2 h. The reaction was stopped by the addition of 50 mg of citric acid and 185 mg of KCl, and after mixing during several minutes the supernatant was transferred to a glass vial, which was sealed after the addition of 1,2-dichlorobenzene as internal standard (10 μ L of a 1/5000 dilution in pentane). The solution was stirred during 15 min at room temperature; meanwhile the volatiles produced during the enzymatic reaction were released into the headspace and adsorbed onto an SPME fiber (PDMS/DVB). The separation and quantification of butyl acetate were done by GC-FID as described before. A calibration curve with butyl acetate was prepared. AAT enzyme activity was expressed as nmol of butyl acetate produced per h and per μg of protein. Protein content was determined (26) using BSA as standard. Determinations were performed in triplicate.

Isolation of AAT Gene from F. chiloensis. Total RNA (1 µg) was extracted from a ripe fruit according to Chang et al. (27), then treated with DNase I amplification grade (Invitrogen), and cDNA synthesized using the BD SMART PCR (Clontech) kit according to the manufacturer's instructions. Primers for the isolation of alcohol acyl transferase cDNA sequence from F. chiloensis were designed using the F. \times ananassa AAT sequence (GenBank accession number AF193789). Primer sequences were AATF = 5'-AAGTCCTGGGGTGCTGTTT-3' and AAT R = 5'CCCTCTTTACCCTTGAAAGTCTC-3'. The PCR product was cloned onto pSCA using the StrataClone PCR Cloning kit according to the manufacturer's instructions (Stratagene, La Jolla, CA) and sequenced at Macrogen Inc. (Seoul, Korea). In order to complete the gene sequence, specific internal primers were designed for 5' and 3'RACE-PCR based on the sequence obtained (AAT-RACE-5' = 5'-AACGCTCATCAGA-TATTGCTTCCA-3' and AAT-RACE-3' = 5'-GGATGGGGGGGGGGGAGGA-CATCATGGATT-3'). RACE-PCR runs were performed using the BD SMART RACE cDNA Amplification kit (Clontech), according to the manufacturer's instructions. The PCR products amplified were cloned and sequenced as described above.

The nucleotide and deduced amino acid sequences were analyzed using Vector NTI Advance v10 software (Invitrogen, 2007). The similarity search and signal peptide predictions were performed using the local alignment tool (BLAST, National Center for Biotechnology Information, Bethesda, MD) and the web based tool Wolf PSORT World Wide Web Prediction Server, respectively (28). The multialignment of amino acid sequences was performed using BioEdit Sequence Alignment Editor v7.0 software (29). The phylogenetic tree was built using MEGA software (version 4; http://www.megasoftware.net) (30) using the neighbor-joining method and Bootstrap analysis (1000 replicates).

Genomic DNA Isolation and DNA Gel-Blot Analysis. Chilean strawberry genomic DNA was extracted from a pool of young leaves (2 g) as described by Murray and Thompson (*31*). For DNA gel blots, 20 μ g aliquots of genomic DNA from Chilean strawberry were digested with the restriction enzymes *Bam*HI, *Hind*III, *Eco*RV and *Eco*RI, fractioned on a 0.7% agarose gel, and transferred to Hybond-N⁺ membranes (Amersham Biosciences, U.K.) using 20× SSC as blotting buffer. Membranes were prehybridized at 42 °C for 4 h in a solution containing 50% deionized formamide, 1% SDS, 5× SSCE, 5× Denhart's solution and 100 μ g mL⁻¹ denatured salmon sperm DNA. The hybridization step was carried out overnight at 42 °C with denatured ³²P-labeled probe with gentle agitation. Washings were performed in SSC, containing 0.1% (w/v) SDS: 2× SSC for 15 min at 42 °C and three times for 15 min at 50 °C with 1× SSC. The blots were exposed, and autoradiograms were scanned in a densitometer (FLA-5100 Imaging System, Fujifilm, Japan).

Probe for DNA gel-blot analysis of *FcAAT1* was designed from a 148 bp region of the gene (nt 1287–1434), consistent in a 3' end portion of 101 bp plus a 3'-UTR sequence of 47 bp. The probe was prepared through PCR reactions with the specific primers qAAT-F/qAAT-R (described in qPCR section) and radiolabeled using $[\alpha$ -³²P]dCTP (Easytides, NEN Life Sciences Products, USA).

Expression Analysis by Real Time PCR (qPCR). Total RNA was extracted from 8 g of F. chiloensis fruit bulk prepared for each developmental stage and other vegetative tissues. It was treated with DNase I amplification grade (Invitrogen), and cleaned using an RNeasy Plant Mini Kit (Qiagen). First strand cDNA synthesis was performed using an AffinityScript QPCR cDNA Synthesis Kit (Stratagene, La Jolla, CA) following the manufacturer's instructions. Three biological replicates for each fruit stage were used. Specific primers for the UTR-3' region of FcAAT1 and the glyceraldehyde 3-phosphate dehydrogenase (FcGAPDH1; as internal control) genes were designed using Vector NTI v10, with high stringency to avoid amplification of unspecific PCR products and secondary structure. Primers were tested by RT-PCR and the amplification products were sequenced in order to check product identity. Primer pair sequences were as follows: qAAT-F (5'- CTGGAATT-GAAGCGTGGGTGAATC-3'), qAAT-R (5'-AAATCGAAACATTG-CACGAGCCAC 3'), GAPDH1-F (5'-TCCATCACTGCCACCCA-GAAGACTG-3') and GAPDH1-R (5'- AGCAGGCAGAACCTTTCC-GACAG-3').

The amplicon sizes were 149 bp for the *FcAAT1* gene and 96 bp for *FcGAPDH1*. The amplification reactions were performed using Brilliant SYBR Green QPCR Master Mix (Stratagene, La Jolla, CA) according to



Figure 1. Changes in weight (**A**), firmness (**B**), total titratable acidity (TA) (**C**) and soluble solid content (SSC) (**D**) during the development of *F. chiloensis* fruit. Data corresponded to the mean \pm SE. Different letters indicate differences between stages (*P* = 0.05).

the manufacturer's instructions, in a DNA engine Opticon 2 Real-Time PCR System (MJ Research, Watertown, MA). PCR conditions were as follows: 94 °C for 10 min; 40 cycles of 94 °C for 15 s, 60 °C for 15 s and 72 °C

	Table 1. A	bundance of Main	Volatile Compounds ($pg g^{-1}$) Produced by	/ Fragaria chil	oensis Fruit at	Different Ri	ipening Stag	es
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						ripeni	ng stage	
compound ^a		$t_{\rm B}^{b}$	LRI ^c	MW	C1	C2	C3	C4
esters								
ethyl acetate ^d	ea	1.60		88.1	4.13 ± 2.11	21.68 ± 7.95	41.09 ± 4.09	52.26 ± 0.01
ethyl butanoate d	eb	3.33		116.1	0.00 ± 0.00	2.11 ± 0.66	1.78 ± 0.07	2.45 ± 0.00
butyl acetate ^{d,e}	ba	3.54		116.0	4.47 ± 0.35	38.64 ± 10.07	130.98 ± 11.25	165.65 ± 11.92
ethyl 2-methyl butanoate d	e2mb	4.34		130.0	0.90 ± 0.06	1.53 ± 0.06	0.42 ± 0.05	0.44 ± 0.00
methyl hexanoate d,e	mhx	5.43	913	130.9	0.57 ± 0.15	1.13 ± 0.28	0.83 ± 0.24	0.95 ± 0.25
ethyl hexanoate d,e	ehx	6.50	976	144.0	0.40 ± 0.11	0.57 ± 0.45	0.64 ± 0.05	1.60 ± 0.44
hexenvl acetate d,e	hxna	6.80	993	142.1	0.85 ± 0.31	1.64 ± 0.62	0.05 ± 0.01	0.06 ± 0.04
hexyl acetate ^{d,e}	hxa	7.07	1008	144.0	3.24 ± 0.30	2.64 ± 0.69	0.55 ± 0.04	0.46 ± 0.13
ethyl heptanoate d	ehp	8.60	1092	158.2	0.10 ± 0.03	0.17 ± 0.08	0.09 ± 0.01	0.06 ± 0.04
hexyl propanoate f	hxpr	8.64	1094	158.0	0.45 ± 0.16	0.43 ± 0.27	0.07 ± 0.01	0.02 ± 0.01
hexyl butanoate f	hxb	9.54	1148	172.1	0.02 ± 0.01	0.04 ± 0.02	0.01 ± 0.00	0.03 ± 0.01
2-hexenyl butanoate f	2hxnb	9.92	1171	170.0	0.02 ± 0.01	0.03 ± 0.01	0.00 ± 0.00	0.01 ± 0.00
benzyl acetate d	bna	10.34	1196	150.2	0.07 ± 0.02	0.05 ± 0.01	0.01 ± 0.00	0.01 ± 0.00
octyl acetate d,e	oa	10.45	1203	172.0	0.07 ± 0.02	0.10 ± 0.02	0.11 ± 0.01	0.10 ± 0.02
hexyl 2-methyl butanoate f	hx2mb	10.71	1221	186.3	0.01 ± 0.00	0.03 ± 0.01	0.03 ± 0.00	0.03 ± 0.01
phenyl ethyl acetate d	pea	11.62	1282	164.0	0.04 ± 0.01	0.06 ± 0.01	0.05 ± 0.01	0.05 ± 0.01
octyl butanoate f	ob	12.24	1325	200.0	0.00 ± 0.00	0.03 ± 0.01	0.01 ± 0.00	0.02 ± 0.00
ethyl 4-decenoate f	e4dec	13.00	1376	200.0	0.02 ± 0.00	0.04 ± 0.02	0.03 ± 0.01	0.03 ± 0.01
2-phenylethyl propanoate f	2-pepr	13.28	1395	178.2	0.00 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00
ethyl 2,4-decadienoate f	e2.4dec	14.26	1466	196.0	0.01 ± 0.00	0.01 ± 0.01	0.01 ± 0.00	0.01 ± 0.00
total acetates					10.87	6/ 81	172.85	221.06
total propapatos					0.45	04.01	0.09	221.90
total butanoates					0.45	3 77	2.00	2.96
total bevanoates					0.00	1 71	1.48	2.50
total hentanoates					0.10	0.17	0.10	0.10
total others					0.02	0.04	0.04	0.04
total esters					15.34	70.94	176.80	227.64
alcohols								
1-butanol ^d	bol	2.00		74.0	11.51 ± 3.16	7.74 ± 2.00	3.04 ± 0.30	1.20 ± 0.15
1-hexanol ^{d,e}	hxol	4.40		102.0	$6.03\pm$	$3.01\pm$	$2.64\pm$	$2.56\pm$
1-heptanol ^d	pol	6.38	967	116.2	28.12 ± 7.44	52.83 ± 10.80	68.54 ± 7.37	72.54 ± 10.24
1-octanol ^{d,e}	ocol	8.18	1069	130.2	0.11 ± 0.05	$\textbf{0.20}\pm\textbf{0.10}$	0.05 ± 0.02	0.00 ± 0.00
total alcohols					45.36	63.78	74.27	76.30
ketones								
2-heptanone ^f	2hpt	5.08		114.0	5.06 ± 0.02	5.04 ± 0.02	5.02 ± 0.02	5.01 ± 0.00
total general					65.76	139.76	256.09	308.95

^a Response factors (× 10³): ea, 2236.38; eb, ba, 91.97; e2mb, 65.64; mhx, 24.35; ehx, hxa, 7.02; hxna, 8.46; ehp, 2.27; hxpr, 2.31; hxb, 0.81; 2hxnb, 0.93; bna, oa, 0.79; hx2mb, 0.30; pea, 1.46; ob, 2-pepr; 0.12; e4dec, 0.14; e2.4dec, 0.16; 2hpt, 112.350; bol, 708.77; hxol, 410.89; pol, 10.00; ocol, 23.00. ^b t_R values correspond to GC-FID chromatographic separation. ^cLRI: linear retention index. ^d Compound identified by GC–MS and confirmed by using commercial standards. ^e Compound described previously in *F. chiloensis* (13). ^f Compound tentatively identified by GC–MS.

for 20 s; and a melting curve from 58 to 95 °C at 0.5 °C increments. A dilution series was built to estimate the amplification efficiency using cDNA mix from fruit samples as template. Each reaction was performed in triplicate, and a negative water control was included in each run. Fluore-scence was measured at the end of each extension step. The amplification efficiency was estimated through a melting curve and amplification products were visualized on agarose gels (1.5% w/v). The relative expression levels were first normalized against the *FcGAPDH1* gene and using fruit sample from stage C1 as calibrator, with a nominal value of 1. The method described by Pfaffl (*32*) was used to make all calculations.

Statistical Analysis. The experiment was conducted using a complete random design with three replicates. Statistical analyses were performed using the SPSS v.14 package. Analysis of variance was performed and significant differences were determined at $P \le 0.05$ (LSD test for quality assessment; Tukey test for volatile measurement and AAT activity; Scheirer–Ray–Hare test, an extension of the Kruskal–Wallis test, for

the expression analysis of FcAAT1) (33). To provide a global overview of volatile compounds, principal component analyses (PCA) were performed.

RESULTS

Characterization of Fruit Stages. Four different developmental stages were defined in *F. chiloensis* fruit following the earlier classification made by Figueroa et al. (23). While stages C1 and C2 correspond to developing fruit, stages C3 and C4 correspond to turning fruit and fully ripe fruit, respectively. As development takes place, the size of the fruit constantly increases, however after the C3 stage the growing of the fruit ceases (**Figure 1A**). As ripening progresses, firmness and titratable acidity reduction were observed (**Figure 1B** and **1C**), while total soluble solids increased constantly from the C1 to the C3 stage (**Figure 1D**).



Figure 2. Loading plot of the first two principal components of PCA for volatiles produced during development of the Chilean strawberry fruit. Labels of volatile compounds as indicated in **Table 1**. PC1 and PC2 accounted for 72.8% of the variance.

Fruit firmness was markedly reduced between the C2 and C3 stages as previously described (23).

Production of Volatiles and AAT Activity during F. chiloensis Development. Many different volatile compounds were identified in the headspace of intact Chilean strawberry fruit, and 25 of them were quantified. The main compounds found were esters, although some alcohols and ketones were also identified (Table 1). Total esters comprised 23.3%, 50.8%, 69.0% and 73.4% of total volatiles in C1, C2, C3 and C4 stages, respectively. The most abundant esters present in fully ripe fruit comprised 98% of total esters, and they have aroma properties with fruity notes: butyl acetate, ethyl acetate, ethyl butanoate and ethyl hexanoate. Among esters, acetates were the most abundant followed by butanoates and hexanoates. Acetates increased their concentration during ripening of the fruit, with maximum production rates at the C4 stage, while butanoates and hexanoates increased between the C1 and C2 stages, remaining high in the following ripening stages.

Total alcohols are abundant in *F. chiloensis* fruit, comprising 69.0%, 45.6%, 29.0% and 25.0% of total volatiles in each developmental stage, respectively. Heptanol is the major alcohol found, followed by butanol and hexanol. Heptanol increased its concentration between stages C1 and C2, and remained high and almost constant during fruit ripening (Table1). The other alcohols (butanol, hexanol and octanol) displayed a reduction in their content during fruit development and ripening, simultaneously with the increment of acetate esters, butanoates and hexanoates.

To provide a general overview of the volatiles, a principal component analysis (PCA) was performed (**Figure 2**). The volatiles produced by the Chilean strawberry fruit were classified into five groups, and the first two components were able to account for 72.8% of the variance. The production profiles for selected volatiles belonging to different groups are shown in **Figure 3**.

Group 1 of compounds comprises volatiles that increased their concentration during development of *F. chiloensis* fruit, with maximum levels in fully ripened fruit, and includes compounds such as ethyl acetate, ethyl butanoate, butyl acetate, ethyl



Figure 3. Production profiles of selected esters during development of *F. chiloensis* fruit. Volatiles belong to different groups according to PCA. The production of volatile compounds was assayed in three replicates per fruit stage, and data corresponds to the mean \pm SE. Different letters indicate differences between stages (*P* = 0.05).

hexanoate, octyl acetate, phenyl ethyl acetate, ethyl 4-decenoate, 1-heptanol, hexyl 2-methyl butanoate and 2-phenylethyl propanoate. Group 2 involves compounds that increased their concentration between C1 and C2 stages and decreased after



Figure 4. Changes in AAT activity during development of *F. chiloensis* fruit. Activity data corresponded to the mean \pm SE of three replicates. Different letters indicate differences between stages (*P* = 0.05).

that: methyl hexanoate, octyl butanoate and hexenyl acetate. Group 3 comprises compounds such as 1-octanol, hexyl acetate and ethyl heptanoate, while group 4 includes compounds like 1-butanol, benzyl acetate, hexyl propanoate, 2-heptanone, 2-hexenyl butanoate, ethyl 2-methyl butanoate and 1-hexanol. Compounds from groups 3 and 4 showed a constant reduction between stages C1 and C3, remaining almost constant after that or displaying a small increase at stage C4. The final group (group 5) comprises volatiles that almost do not change their concentration during development such as ethyl 2,4-decadienoate and hexyl butanoate.

Since esters are important for aroma and a significant increase in total ester production was observed during development of the Chilean strawberry fruit, we focused our analysis on ester biosynthesis by the AAT enzyme. *In vitro* AAT activity, assayed by the capacity to produced butyl acetate, showed an important increment during *F. chiloensis* development, with a high level of activity at C3 and C4 stages (**Figure 4**). A good correlation was found between AAT activity and the total content of esters (r =0.81); especially a high correlation was found between AAT activity and acetates (r = 0.81) and hexanoates (r = 0.93).

Isolation of FcAAT1 and Phylogenetic Analysis. An AAT gene was isolated from a ripe F. chiloensis fruit using specific primers matching an AAT gene from $F. \times$ ananassa. A fragment of 545 bp with high homology to other AAT genes from the Fragaria genus was obtained, and used as template to design internal primers for 5' and 3'-RACE-PCR. A 793 bp 5' RACE fragment (with 291 bp overlap with the original fragment) and a 781 bp 3'-RACE fragment (with 215 bp overlap) were isolated using these primers. Therefore, a composite cDNA sequence of 1,620 bp called FcAAT1 (GenBank accession number FJ548611) was generated after assembling of all fragments. Analysis of the FcAAT1 sequence revealed an ORF of 1,384 bp, and a deduced polypeptide sequence of 450 amino acids with a molecular weight of 50.4 kDa. The sequence also contained 35 bp and 234 bp of 5' and 3'-UTR, respectively. The coding region displayed the three motifs which are characteristic of most AAT previously described: LALYYPLSGR, HKLID and DFGWG (Figure 5A). A multiple alignment of *FcAAT1* with other fruit-specific AAT sequences showed a low level of amino acid conservation, restrained to the functionally and structurally important motifs.

A phylogenetic tree was built from the multiple alignment of deduced amino acid sequences of fourteen AATs (Figure 5B). The

clustering pattern visualized in the phylogenetic tree reproduces three subgroups. Interestingly, the grouping pattern incorporates FcAATI into subgroup II, next to other AATs from the *Fragaria* genus, and in a divergent position with respect to some ripeningrelated AATs from other fruit species (subgroup III) such as melon, pear and apples.

DNA Gel-Blot Analysis. In order to analyze the complexity of Chilean strawberry's alcohol acyltransferase gene family, DNA gel-blot of genomic DNA digested with four different restriction enzymes was hybridized with a specific probe obtained from the divergent region of *FcAAT1* (Figure 6). DNA gel-blot analysis revealed at least two hybridizing bands with all the restriction enzymes tested, all of them ranging between 2.0 kb and 23.1 kb approximately. The digestion product of *Bam*HI showed two hybridizing bands over 9.4 kb while the other three enzymes showed smaller bands. *Hind*III restriction pattern exhibited three major hybridizing bands and one weaker around 2.4 kb, while *Eco*RI digestion showed one major (around 5.0 kb) and four weaker bands. An *in silico* analysis of the cDNA showed no restriction sites for *Bam*HI, *Eco*RI and *Eco*RV, although two restriction sites were found for *Hind*III.

FcAAT1 Expression Analysis during Fruit Development. The expression of FcAAT1 was analyzed by qPCR in fruit samples at different developmental stages, as well as in different vegetative tissues (Figure 7). Almost no transcript accumulation was observed in fruit at the first stage of development; however, the expression level increased concomitantly with the ripening progress, showing a high level of FcAAT1 transcripts at C3 and C4 stages (Figure 7A). In the other vegetative tissues analyzed, flowers, runners, stem and leaves, a very low transcript accumulation was observed compared to ripe *F. chiloensis* fruit (Figure 7B).

DISCUSSION

Chilean strawberry is a new and commercially promising fruit crop in Chile, but unfortunately little information exists concerning its ripening physiology. Our research group has initiated a study on aspects which are relevant for fruit quality, such as softening (23,34)and aroma formation. Among the volatiles found in intact *F. chiloensis* fruit, esters are important due to their abundance and aroma properties. Therefore, we decided to analyze the production profile of esters during development of the fruit.

Using headspace-SPME we were able to identify more than 40 different volatile compounds in intact F. chiloensis fruit, 25 of them were quantified. Volatile components of the Chilean strawberry fruit were dominated by esters, mainly by butyl acetate and ethyl acetate, which increased during ripening. Among the volatiles quantified, only six esters and two alcohols were reported previously in F. chiloensis fruit (13). Early studies performed in fruit extracts reported differences in the aroma patterns between different strawberry cultivars (35), and also differences between $F. \times$ ananassa and wild species such as F. chiloensis (13). Our results with intact fruit confirm that issue. Some esters found in F. chiloensis fruit like ethyl acetate, methyl butanoate, 2-methyl acetate, octyl acetate, octyl butanoate, hexyl acetate, ethyl heptanoate, 2-hexenyl butanoate, benzyl acetate and hexyl 2-methyl butanoate were also described in several F. \times ananassa cultivars (7, 9, 36, 37). However, we found in F. chiloensis some esters which have not been described previously in $F. \times ananassa$, such as hexyl propanoate, ethyl 4-decenoate, 2-phenylethyl propanoate and ethyl 2,4 decadienoate; nevertheless they have been described before in apple fruit and strawberry wine (38, 39) On the other hand, the same type of alcohols was found in both species, $F. \times$ ananassa and F. chiloensis.

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- T	PeaaT1	MPY	TRACTTORYT	TTE. CCCT.	LOPVELSELD	OL TODA VUDA	UPPUDTTP	HUPNI POTLA	DEPOSTSET	AT WYDT CHI	UWNNT	VIDNEEPEVE	VIENOVNCOM	TOPLALOWTE
	PCAALL	MOR	IBUSIISKII	THE CHOCOD	LOPYKLSELD	QUIPPAIVPN	VPPIPIIS	HVENDPQTDA	DURQUUSEIN	ADTIPLEGR-	VKNNL	TIDNPELEVP	TIMAQVACDA	IDF DREGKIE
	PVAAL	ADA	TRUSTISKAT	THE GROOM	LODYNIMIC	QUIPPBIVPM	VPPIPIIG	PAVENLOTLA	DIRALBEIT	TETTPESCA-	THE PARTY NEW PARTY	TIDDFEREVP	TIMARVICON	NUPLRUPKIE
	FAAAT	REK	TENSINSKHT	INS-SISSIP	LUPIKLILLD	QLIPPAIVPI	VFF1P11D	HDFNLPQTLA	DERQAESET	TLITPLSGR-	VKNNL	TIDDFEECVP	TLEARVINCEM	TOFLELERIE
	MPAATI	-MMSFSV	LOWKRLOPEL	ITE-AKSTPQ	ETKFLSDIDD	QESTRAGILI	INCYKDNP	SLNKNRNPVK	AIREALSRA	AAAAbrydan	REGPNRKL	VVDCNGEEIL	FVDASADVTL	RÖFCOKIFAA
	MdAAT2	-MMPFSV	LOWKRLQLEL	ITE-AKPTLQ	EAKFLSDIDD	QEGLRFQVPV	IMCYKDNP	SLNKNCNPVK	VIREALSRAM	VYYYPLACERL	KEGPNRKL	MVDCNGECIL	FVBASADVTL	EQLGDKILPP
	PCAAT1	-MMSLSV	LOWKRLQPEL	ITE-AKPTPQ	ETKFLSDIDD	QEGLRFQLPV	INCYKDNP	SLNKNRNPIK	VIKEALSRAD	VYYYPLAGEL	REGP NRKL	MVNCNGEGIL	FVEASADVTL	EQLGDKILPP
	RhAAT	MEK	IEVSIISRDT	IKE-SAASSS	LHPYKLSIID	QFTPTTYFPV	IFFYPITD	RVFNLPQTLT	DLKNTVSQAD	TLYHPLSOR-	IKNNL	YIDDFEASIP	YLEARVNFHM	IDFLRLPKIE
	MSAAT1	MS	FAUTRTSRSL	VTE-CGVTPT	GSLGLSAIDR	VPGLRHMVRS	LHVFR	QGREPAR	IIREALSKAD	VKYYPFAGRF	VDDPEGGGEV	RVACTGEGAW	FVEAKADCSL	EDVKYLDLP-
	VpAAT1	-MAEKASSLM	FNVRRHEPEL	ITE-AKPTPR	EIKLLSDIDD	QDGLRFQVPI	IQFYKNNS	S-MQGKNPAK	IIKSALAETL	VHYYPLAGEL	REGF GRKL	MVECTGECIL	FIDADADVTL	HEFGDDLPPP
	CmAAT1	DFS	FHURKCOPEL	IAE-ANPTPY	EFKQLSDVDD	QQSLRLQLPF	VNIYPHNP	S-LEGRDPVK	VIKEAIGKAL	VFYYPLAGRL	REGPGRKL	FVECTGEGIL	FIDADADVSL	EEFWDTLPYS
	CmAAT2	METMQTIDFS	FOURKCOPEL	IAE-ANPTPY	EFKQLSDVDD	QQSLRFQLPL	VNIYHHNP	S-LEGRDPVK	VIKEAIAKA	VFYYPLAGEL	REGPGRKL	FVECTGECIL	FIDADADVSL	EQFRDTLPYS
	CmAAT3	-MASSLV	FQUQRSQPQL	IPE-SDPTPH	EFKQLSDIDD	QEGLRFQIPV	IQFYRHDP	R-MAGTDPAR	VIKEAIAKAN	VFYYPFAGRL	REGP GRKL	FVECTGECVM	FIRADADVSL	EQFGDALQPP
	CmAAT4		MEWKVLSKET	IIESSPTPPH	LQPLNLSLLD	QLSPMLYIPL	LLFYPMKKSY	QHQDHNKAIA	TLKTSLSKTL	SRFYLLAGR-	IIG-K	SIHCNDKGAV	FMEATINSNM	FDILKEPNNE
	CUBERT	-MAHDQ-SLS	FEWCRRKPEL	IRE-AKQTPH	EFKKLSDVED	QEGLRFQIPV	IQFYKHNN	ESMQERDPVQ	VIREGIARA	VYYYPFAGRL	REVD GRKL	VVECTGEGVM	FIDADADVTL	EQFGDALQPP
	Cbbeat		MNWTMHSKKL	LKESIPTPNH	LQKLNLSLLD	QIQIPFYVGL	IFHYETLS	DNSDITLS	KLESSLSETL	TLYYHVAGRY	NGTDC	VIECNDOCIG	YVOTAFDVEL	HQFLLGEESN
		14	0 150	160	17	0 18	0 19	0 200	21	0 220	230	240	0 25	260
	FcAAT1	CLNEFVSIKP	FSMEAISDER	YPLLGVOVNV	FDSG-IAIGV	SLSOKLIDGR	TAYCELKSWG	AVFRGCR		-EDVIHPSLS	EAALLFPPRD	DLPEKYADQM	EGLWFAGKKV	ATRRFVFGAK
	FVAAT	CLNEFVPIKP	FSMEAISDER	YPLLGVOVNI	FNSC-IAIGV	SVSUKLIDGR	TSDCOLKSWC	AVFRGSR		-DKIIHPNLS	QAALLFPPRD	DLPEKYARQM	EGLWFVGKKV	ATRRFVFGAK
	FaAAT	CLNEFVPIKP	FSMEAISDER	YPLLGVOVNV	FDSC-IAIGV	SVSHKLIDGG	TADCELKSWG	AVFRGCR		-ENIIHPSLS	EAALLFPPRD	DLPEKYVDQM	EALWFAGKKV	ATRRFVFGVK
	MPAAT1	CPLLE-EFLY	NFPGSDGIID	CPLLLIOVIC	LTCCGFILAL	RLNHTMCHAA	GLLLELTAIA	EMARGAHA	PSILPV	WERELLFARD	PPRITCAHHE	YEDVIGHSDG	SYASSNQSNM	VQRSFYFGAK
	MdAAT2	CPLLE-EFLF	NFPGSDGIIG	CPLLLVOVTC	LTCCGFILAL	RVNHTMCDAP	GLLLELTAIA	EMARGAHA	PSILPV	WERELLFSRD	PPRITCAHHE	YEDVIDHSDG	LYASSNQSNM	VQRSFYFGAK
	PcAAT1	CPLLE-EFLF	NFPGSDGIIG	CPLLLVOVTC	LTCCGFILAL	RLNUTMODAT	GLLMELTAIT	EMGEGADA	PSILPV	WERELLFARD	PPRITCAHYE	YEDVIDHSDG	SYAFSNQSNM	VQRSFYFGAK
	RhAAT	WLNEFVPMAP	YRKETIS-EF	LPLLGIOVNI	FDSC-IAIGV	SFSHKINDGQ	TASCELKSWV	AIFEGYR		-NKIIHPNLS	QAALLLPSRD	DLPEKYVAMM	ERMWFGEKKV	VTRRFVFDAK
	MSAAT1	-LMIPEDALL	PKPCPGLNPL	DLPLMLOVTE	FVGGGFVVGL	ISVHTIADGL	GVVQRINAVA	EIARGLPK	PTVEPA	WSREVIPN	PPKLPPGGPP		VFPSFKL	LHATVDLSPD
	VPAAT1	FPCLV-ELLY	DVPGSSGIID	TPLLLIOVTR	LKCCGFIFAL	RLNHTMSDAS	GLVQENTAVG	EMARGORS	LSIQPV	WERHLLNARD	PPRVTHIHHE	YDDLEDTKG-	TIIPLDDM	VHRSFFFGPS
	CmAAT1	LSSMQNNIIH	NALNSDEVLN	SPLLLIGVTR	LKCCGFIFGL	CFNHTMADGF	GIVORMKATA	EINEGAFA	PSILPV	WQRALLTARD	PPRITFRHYE	YDQVVDMKS-	GLIPVNSK	IDQLFFFSQL
	CmAAT2	LSSMENNIIH	NSLNSDGVLN	SPLLLIOVTR	LKCCGFIFGI	HFDUTMADGF	GIAQUMKAIA	EIARGAFA	PSILPV	WQRALLTARD	PPRITVRHYE	YDQVVDTKS -	TLIPANNM	IDRLFFFTQR
	CmAAT3	FPCLE-EPLF	DVPNSSGVLD	CPLLLIOVTR	LKCGGFIFAL	RLNOTMSDAS	GLVQEMMAVG	EMARGATA	PSVRPV	WQRALLNARD	PPKVTCHHRE	YDEVVDTKG-	TIIPLDDM	AHRSFFFGPS
	CmAAT4	VLTKLLPCS -	LLCNTKPIEE	YPOIVVCANI	FECCGIAISL	CLINKLIDAA	TFCCGLRSWA	TINRELLSLD	HSSPNNNMVC	VDYKSFSSLF	PQTNLLPFHQ	SLINNDKAVV	PPSSIFNRKR	RFQRFVFRSE
	CDBEBT	FPCFD-QLLF	DVPGSGGILD	SPLLLIGVTR	LKCCSFIFAL	RLNHTMAHAA	GIVLEMKAVG	EMARGAAT	PSTLPV	WDRHILNARV	PPQVTFNHRE	YEEVKGT	IFTPFDDL	AHRSFFFGST
	CEBEAT	NLDLLVGLSG	FLSETET	PPLAATCLNM	FKCGGLVIGA	QFNHIIGOMF	TMSTEMNSWA	KACEVGIK		EVAHPTF	GLAPLMPSAK	VLNIPPPPS-	FEGVKF	VSKRFVFNEN
				10000	3.575			100						
		27	280	290	30	0 31	0 32	0 330	34	0 350	360	37	38	390
	FCAAT1	AISSIQDEAK	SES	-VPKPSRVQA	VTGFLWKHLI	AASRALTSGT	TSTRLSIAAQ	AVNLRTRMNM	ETVLDNATCH	LIWWAQAILE	LSHT TPEI	SDLKLCDLVN	LLNGSVKQCN	GDYFETFKGK
	FVAAT	AISVIQDEAK	SES	-VPKPSRVQA	VISFLWKHLI	ATSRALTSGT	TSTRLSIATQ	VVNIRSRRNM	ETVWDNAIGN	LIWFAPAILE	LSHT TLEI	SDLKLCDLVN	LLNGSVKQCN	GDYFETFMGK
	FAAAT	AISSIQDEAK	SES	-VPKPSRVHA	VIGFLWKHLI	AASRALTSGT	TSTRLSIAAQ	AVNLRTRMMM	ETVLDNATCN	LFWWAQAILE	LSHT TPEI	SDLKLCDLVN	LLNGSVKQCN	GDYFETFKGK
	MpAAT1	EMRVLRKQIP	PHL	-ISTCSTFDL	ITACLWKCRT	LALNI NPK	EAVRVSCIVN	ARGKHNN	VRLPLGYYGN	AFAFPAAISK	AEPL	CKNPLGYALE	LVKKAKATMN	EEYLRSVAD-
	MdAAT2	EMRVLRKQIP	PHL	-ISTCSTFDL	ITACLWKCRT	LALNI NPK	EAVRVSCIVN	ARGKHNN	VRLPLGYYCN	AFAFPAAISK	AEPL	CKNPLGYALE	LVKKAKATMN	EEYLRSVAD-
	PcAAT1	EMRVLRKQIP	PHL	-ISTCSTFDL	ITACLWKCRT	LVLKI NPK	QAVRVSCIVN	AR GKHNN	VHIPLGYYGN	AFAFPAAVSK	AEPL	CKNPLGYALE	LVKKAKATMN	EEYLRSVAD-
	RhAAT	AISALQDECK	SEY	-VPKPSRVQA	LTGFLWKHQL	AASRALSSG-	TSTRFSVASQ	TVNLRSKMNM	KTTLDNAIGN	IFLWASARLD	LNDT APGS	SDLKLCDLVN	LLNESIKEFN	SDYLEILKGK
	MSAAT1	HIDHVKSRHL	ELT	- GORCSTFDV	AIANLWQSRT	RAINLDPG	VDVHVCFFAN	TRHLLROVVL	LPPEDGYYCN	CFYPVTATAP	SGRI	ASAELIDVVS	IIRDAKSRLP	GEFAKWAAG-
	VpAAT1	EMAAIRRLVP	AHF	-HRSTT-SEV	LTAYLWRCYT	IALOPDPE	EEMRVICVVN	SRTELN-	PPLPTGFYCN	GIAFPAAISO	AKK I	CENFFGYTLO	LVKOTKVDVT	EEYMRSAAD-
	CmAAT1	QISTLEQTLP	AHL	-HDCPS-FEV	LTAYVWRLRT	IALQF KPE	EEVRFLCVMN	LRSKID-	IPLGYYGN	AVVVPAVITT	AAKL	CGNPLGYAVD	LIRKAKAKAT	MEYIKSTVD-
		and the second s			A & A STREET, SALE		PRUDPL CUMM	LRSKID-	IPLGFYCN	AIVFPAVITT	VAKI.	CONPLOYAVD	LIRKAKAKAT	KEYIKSMVD-
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	CmAAT2 CmAAT3 CmAAT4	QISTLRQTLP EISAIRKALP AILDLKAKAK	AHL SHL SCD	-HDCSS-FEV -RQCSS-FEV -IPNPTCVET	LTACLWRFRT LTCFIWKYLM	ISLQPDPE KVADDG	EEVRVLCIVN	SRSEFN- VVNIR-EMLE	PPLPTGYYGN PSLGEVSLGN	AFAFPVALTT IMWGTVAHHF	AGKL STTRNEEF	CQNPLGYALE EGLELSKLVS	LVRKAKADVT LLROSFKKIN	EDYMKSVAD- KDYIKELIMG
	CmAAT2 CmAAT3 CmAAT4 CbBEBT	QISTLEQTLP EISAIRKALP AILDLKAKAK EISAMRKQIP	AHL SHL SCD PHL	-HDCSS-FEV -RQCSS-FEV -IPNPTCVET -RSCSTTIEV	LTACLWRFRT LTCFIWKYLM LTACLWRCRT	IAFQLKPE ISLQPDPE KVADDG LAIKPNPD	EEVRVLCIVN DSQRPSTLSH EEVRMICIVN	SRSKFN- VVNIR-KMLE ARSKFN-	PPLPTGYYGN PSLGEVSLGN PPLPDGYYGN	AFAFPVALTT INWGTVAHHF AFAIPAAVTT	AGKL STTRNEEF AGKL	CQNPLGYALE EGLELSKLVS CNNPLGFALE	LVRKAKADVT LLRQSFKKIN LIRKAKREVT	EDYMKSVAD- KDYIKELIMG EEYMHSVAD-
	CmAAT2 CmAAT3 CmAAT4 CbBEBT CbBEAT	QISTLROTLP EISAIRKALP AILDLKAKAK EISAMRKQIP AITRLRKEAT	AHL SHL SCD PHL EEDGDGDDDQ	-HDCSS-FEV -RQCSS-FEV -IPNPTCVET -RSCSTTIEV KKKRPSRVDL	LTACLWRERT LTCFIWKYLM LTACLWRCRT VTAFLSKSLI	IAFQLKPE ISLQPDPE KVADDG LAIKPNPD EMDCAK-KEQ	EEVRVLCIVN DSQRPSTLSH EEVRMICIVN TKSRPSLMVH	SRSEFN- VVNIR-EMLE ARSEFN- MMN-LRERTE	PPLPTGYYGN PSLGEVSLGN PPLPDGYYGN LALENDVSGN	AFAFPVALTT IMWGTVAHHF AFAIPAAVTT FFIVVNAESK	AGKL STTRNEEF AGKL ITVAPKITDL	CONPLGYALE EGLELSKLVS CNNPLGFALE TESLGSACGE	LVRKAKADVT LLRQSFKKIN LIRKAKREVT IISEVAKVDD	EDYMKSVAD- KDYIKELIMG EEYMHSVAD- AEVVSSMVLN
	CmAAT2 CmAAT3 CmAAT4 CbBEBT CbBEAT	QISTLROTLP EISAIRKALP AILDLKAKAK EISAMRKQIP AITRLRKEAT	AHL SHL PHL EEDGDGDDDQ	-HDCSS-FEV -RQCSS-FEV -IPNPTCVET -RSCSTTIEV KKKRPSRVDL	LTACLWRERT LTCFIWRYLM LTACLWRCRT VTAFLSKSLI	IAFQLKPE ISLQPDPE KVADDG LAIKPNPD EMDCAK-KEQ	EEVRVLCIVN DSQRPSTLSH EEVRMICIVN TKSRPSLMVH	SRSKFN- VVNIR-KMLE ARSKFN- MMN-LRKRTK	PPLPTGYYGN PSLGEVSLGN PPLPDGYYGN LALENDVSGN	AFAFPVALTT INWGTVAHHF AFAIPAAVTT FFIVVNAESK	AGKL STTRNEEF AGKL ITVAPKITDL	CQNPLGYALE EGLELSKLVS CNNPLGFALE TESLGSACGE	LVRKAKADVT LLRQSFKKIN LIRKAKREVT IISEVAKVDD	EDYMKSVAD- KDYIKELIMG EEYMHSVAD- AEVVSSMVLN
	CmAAT2 CmAAT3 CmAAT4 CbBEBT CbBEAT	QISTLROTLP EISAIRKALP AILDLKAKAK EISAMRKQIP AITRLRKEAT 40	AHL SHL SCD PHL EEDGDGDDDQ 0 410	-HDCSS-FEV -RQCSS-FEV -IPNPTCVET -RSCSTTIEV KKKRPSRVDL 420	LTACLWRERT LTCFIWKYLM LTACLWRCRT VTAFLSKSLI	IAFQLKPE ISLQPDPE KVADDG LAIKPNPD EMDCAK-KEQ	EEVRVLCIVN DSQRPSTLSH EEVRMICIVN TKSRPSLMVH	SRSKFN- VVNIR-KMLE ARSKFN- MMN-LRKRTK 0 460	PPLPTGYYGN PSLGEVSLGN PPLPDGYYGN LALENDVSGN 47	AFAFPVALTT INWGTVAHHF AFAIPAAVTT FFIVVNAESK 0 480	AGKL STTRNEEF AGKL ITVAPKITDL	CQNPLGYALE EGLELSKLVS CNNPLGFALE TESLGSACGE	LVRKAKADVT LLRQSFKKIN LIRKAKREVT IISEVAKVDD	EDYMKSVAD- KDYIKELIMG EEYMHSVAD- AEVVSSMVLN
	CmAAT2 CmAAT3 CmAAT4 CbBEBT CbBEAT	QISTLROTLP EISAIRKALP AILDLKAKAK EISAMRKQIP AITRLRKEAT 40	AHL SHL SCD PHL EEDGDGDDDQ 0 410	-HDCSS-FEV -RQCSS-FEV -IPNPTCVET -RSCSTTIEV KKKRPSRVDL 0 420	LAATVWRLRT LTACLWRPRT LTCFIWRYLM LTACLWRCRT VTAFLSKSLI	IAFQLKPE ISLQPDPE KVADDG LAIKPNPD EMDCAK-KEQ	EEVRPLCIVN DSQRPSTLSH EEVRMICIVN TKSRPSLMVH	SRSEFN- VVNIR-KMLE ARSEFN- MMN-LRERTE 0 460	PPLPTGYYGN PSLGEVSLGN PPLPDGYYGN LALENDVS <mark>GN</mark> 47	AFAFPVALTT INWGTVAHHF AFAIPAAVTT FFIVVNAESK 0 480	AGKL STTRNEEF AGKL ITVAPKITDL	CQNPLGYALE EGLELSKLVS CNNPLGFALE TESLGSACGE	LVRKAKADVT LLRQSFKKIN LIRKAKREVT IISEVAKVDD	EDYMKSVAD- KDYIKELIMG EEYMHSVAD- AEVVSSMVLN
	CmAAT2 CmAAT3 CmAAT4 CbBEBT CbBEAT FcAAT1	QISTLRQTLP EISAIRKALP AILDLKAKAK EISAMRKQIP AITRLRKEAT 40 	AHL SHL SCD PHL EEDGDGDDDQ 0 410 	-HDCSS-FEV -RQCSS-FEV -IPNPTCVET -RSCSTTIEV KKKRPSRVDL 0 42(PAPDIYLFSS	LAALVWRLRT LTACLWRFRT LTCFIWKYLM LTACLWRCRT VTAFLSKSLI 0 43 	IAPQL - KPE ISLQP - DPE KVA DDG LAIKP - NPD EMDCAK - KEQ 0 44 	EEVRVLCIVN DSQRPSTLSH EEVRMICIVN TKSRPSLMVH 0 45 	SRSEFN- VVNIR-KMLE ARSEFN- MMN-LRERTE 0 460 	PPLPTGYYGN PSLGEVSLGN PPLPDGYYGN LALENDVSGN 47 QCGSG-IEAW	AFAFPVALTT IMWGTVAHHF AFAIPAAVTT FFIVVNAESK 0 480 	AGKL STTRNEEF AGKL ITVAPKITDL 0 490 	CQNPLGYALE EGLELSKLVS CNNPLGFALE TESLGSACGE	LVRKAKADVT LLRQSFKKIN LIRKAKREVT IISEVAKVDD 0 51(EDYMKSVAD- KDYIKELIMG EEYMHSVAD- AEVVSSMVLN
	CmAAT2 CmAAT3 CmAAT4 CbBEBT CbBEAT FcAAT1 FvAAT	QISTLRQTLP EISAIRKALP AILDLKAKAK EISAMRKQIP AITRLRKEAT 400 EGYGRMCEYL EGYGSMCEYL	AHL	-HDCSS-FEV -RQCSS-FEV -IPNPTCVET -RSCSTTIEV KKKRPSRVDL 420 420 	LTACLWRERT LTCFIWKYLM LTCCLWRCRT VTAFLSKSLI 43 	IAPQLKPE ISLQPDPE KVADDG LAIKPNPD EMDCAK-KEQ 0 444 	EEVRVLCIVN DSQRPSTLSH EEVRMICIVN TKSRPSLMVH 0 45 	SRSKFN- VVNIR-KMLE ARSKFN- MMN-LRKRTK 0 460 SCKFIILVPT FCNLTLVPT	PPLPTGYYGN PSLGEVSLGN PPLPDGYYGN LALENDVSGN 47 	AFAFPVALTT INWGTVAHHF AFAIPAAVTT FFIVVNAESK 0 480 VNLEEEKMAM VNLEEEKMAM	AGKL STTRNEEF AGKL ITVAPKITDL 0 490 	CQNPLGYALE EGLELSKLVS CNNPLGFALE TESLGSACGE 	LVRKAKADVT LLRQSFKKIN LIRKAKREVT IISEVAKVDD 0 51(EDYMKSVAD- KDYIKELIMG EEYMHSVAD- AEVVSSMVLN % I
	CmAAT2 CmAAT3 CmAAT4 CbBEBT CbBEAT FcAAT1 FvAAT FaAAT	QISTLRQTLP EISAIRKALP AILDLKARAK EISAMRKQIP AITRLRKEAT 40 	AHL SKL PHL EEDGDGDDDQ 0 410 	-HDCSS-FEV -RQCSS-FEV -IPNPTCVET -RSCSTTIEV KKKRPSRVDL 420 	LAAIVWALRT LTACLWRFRT LTCFIWKYLM LTACLWRCRT VTAFLSKSLI) 43 	IAPQLKPE ISLQPDPE KVADDG LAIKPNPD EMDCAK-KEQ 0 44 FGWGRTSW FGWGRTSW FGWGRTSW	EEVRVLCIVN DSQRPSTLSH EEVRMICIVN TKSRPSLMVH 0 45 	SRSKFN- VVNIR-KMLE ARSKFN- MMN-LRKRTK 0 460 SCKFIILVPT FCNLTLVPT SCKFIILVPT	PPLPTGYYGN PSLGEVSLGN PPLPDGYYGN LALENDVSGN 47 QCGSG-IEAW QCGSG-IEAW QCGSG-IEAW	AFAFPVALTT IMMGTVAHHF AFAIPAAVTT FFIVVNAESK 0 480 	AGKL STTRNEEF AGKL ITVAPKITDL 0 490 	CQNPLGYALE EGLELSKLVS CNNPLGFALE TESLGSACGE 50 ASPKTLI ASPKTLISRY ASPKTLI	LVRKAKADVT LLRQSFKKIN LIRKAKREVT IISEVAKVDD 0 51(EDYMKSVAD- KDYIKELIMG EEYMHSVAD- AEVVSSMVLN 0 % I %5. 94.
	CmAAT2 CmAAT3 CmAAT4 CbBEBT CbBEAT FcAAT1 FvAAT FvAAT FaAAT MpAAT1	QISTLRQTLP EISAIRKALP AILDLKAKAK EISAMRKQIP AITRLRKEAT 40 EGYGRMCEYL EGYGRMCEYL EGYGRMCEYL	AHL SHL EEDGDGDDDQ 0 41(DFQRTMSSME DFQRTMSSME DFQRTMSSME LVLRGRPQYS	-HDCSS-FEV -RQCSS-FEV -IPNPTCVET -RSCSTTIEV KKKRPSRVDL 42(PAPDIYLFSS PAPEIYLFSS STGSYLIVSD	LTACLWRERT LTCFIWKYLM LTCFIWKYLM LTACLWRCRT VTAFLSKSLI 0 43 	IAPQLKPE ISLQPDPE KVADDG LAIKPNPD EMDCAK-KEQ 0 44 FGWGRTSW FGWGRTSW FGWGRTSW FGWGQPVF	EEVRVLCIVN DSQRPSTLSH EEVRMICIVN TKSRPSLMVH 0 45 IGVAGKIESA IGVAGKIESA AGPVKA	SRSKFN- VVNIR-KMLE ARSKFN- MMN-LRKRTK 0 460 SCKFIILVPT FCNLTTLVPT SCKFIILVPT .LDLISFYVQ	PPLPTGYYGN PSLGEVSLGN PPLPDGYYGN LALENDVSGN 0 47 	AFAFPVALTT IMMGTVAHHF AFAIPAAVTT FFIVVNAESK 0 480 	AGKL STTRNEEF AGKL ITVAPKITDL 0 490 	CQNPLGYALE EGLELSKLVS CNNPLGFALE TESLGSACGE) 501 	LVRKAKADVT LLRQSFKKIN LIRKAKREVT IISEVAKVDD 0 51(EDYMKSVAD- KDYIKELIMG EEYMHSVAD- AEVVSSMVLN % I 85. 94. 15.
	CMAAT2 CMAAT3 CMAAT4 CbBEBT CbBEAT FCAAT1 FVAAT FAAAT MpAAT1 MdAAT2	QISTLEQTLP EISAIRKALP AILDLKAKAK EISAMRKQIP AITRLRKEAT 40 	AHL SHL EEDGDGDDDQ 0 410 	-HDCSS-FEV -RQCSS-FEV -IPNPTCVET -RSCSTTIEV KKKRPSRVDL 42(PAPDIYLFSS PAPEIYLFTS PAPEIYLFTS STGSYLIVSD STGSYLIVSD	LTACLWRFRT LTCFIWKYLM LTACLWRCRT VTAFLSKSLI 43 	IAPQL - KPE ISLQP - DPE KVA DDG LAIKP - NPD EMDCAK - KEQ 0 44 	EEVRVLCIVN DSQRPSTLSH EEVRMICIVN TKSRPSLMVH 0 45 	SRSKFN- VVNIR-KMLE ARSKFN- MMN-LRKRTK 0 46(SCKFILVPT FCNLTTLVPT SCKFILVPT -LDLISFYVQ -LDLISFYVQ	PPLPTGYYGN PSLGEVSLGN PPLPDGYYGN LALENDVSGN 0 47 	AFAFPVALTT IMMGTVAHHF AFAIPAAVTT FFIVVNAESK 0 480 VNLEEEKMAM VNLEEEKMAM VNLEEEKMAM LVPMCLPSSA LVPMCLPSSA	AGKL STTRNEEF AGKL ITVAPKITDL 0 490 	CQNPLGYALE EGLELSKLVS CNNPLGFALE TESLGSACGE ASPKTLI ASPKTLISRY ASPKTLISRY ASPKTLI ITQ-EPKEDI ITQ-EPKEDI	LVRKAKADVT LLRQSFKKIN LIRKAKREVT IISEVAKVDD 0 51(EDYMKSVAD- KDYIKELING EEYMHSVAD- AEVVSSMVLN 0 % I 85. 94. 94. 15.
	CmAAT2 CmAAT3 CmAAT4 CbBEBT CbBEAT CbBEAT FcAAT1 FvAAT FaAAT MdAAT2 FcAAT1	QISTLECTLE EISATEKALP AILDLKAKAK EISAMEKQIP AITRLEKEAT 40 	AHL SHL PHL EEDGDGDDDQ 0 410 	-HOCSS-FEV -RQCSS-FEV -RQCSS-FEV -RCSSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCSTIEV -RCST	LTACLWRERT LTACLWRERT LTACLWRCRT VTAFLSKSLI 43 	IAPQLKPE ISLQPDPE ISLQPDPG LAIRPNPD EMDCAK-KEQ 0 44 	EEVRVLCTVN DSQRPSTLSH EEVRWICTVN TKSRPSLMVH 0 45 	SRSKFN- VVNIR-KMLE ARSKFN- MMN-LRKRTK 0 460 	PPLPTGYYGN PSLGEVSLGN PPLPDGYYGN LALENDVSGN 0 47 	AFAPPVALT IMWGTVAHHF AFAIPAAVTT FFIVVNAESK 0 480 480 VNLEEEKMAM VNLEEEKMAM VNLEEEKMAM LVPMCLPSSA LVPMCLPSSA	AGKL STTRNEEF AGKL ITVAPKITDL 0 490 	CQNPLGYALE EGLELSKLVS CNNPLGFALE TESLGSACGE ASPKTLI ITQ-EPKEDI ITQ-EPKEDI ITT-GT	LVRKAKADVT LLRQSFKKIN LIRKAKREVT IISEVAKVDD 0 510 	EDYMKSVAD- KDYIKELIMG EEYMHSVAD- AEVVSSMVLN 0 % I 85. 94. 94. 15.
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	CmAAT3 CmAAT4 CmAAT4 CbBEBT CbBEBT CbBEAT FcAAT1 FcAAT FcAAT FcAAT FcAAT1 RhAAT McAAT1 VpAAT1 CmAAT1 CmAAT3 CmAAT3	GISTINGTLE EISATEKALP AILDIKARAK EISAMEKGIP AITRLEKEAT 40 	AHL SCD PHL EEDGDGDDDQ 0 410 	-HOCSS-FEV -RQCSS-FEV -RQCSS-FEV -RSCSTIEV KKKRPSRVDL 	LAACUWERET LTACLWERET LTACLWERET UTAFLSESLI 43 	IAPQLKPE ISLQDPE KVADDE LAIRPMPD EMDCAK-KEQ 0 441 FGWGRTSW FGWGRTSW FGWGRTSW FGWGQPVF FGWGQPVF FGWGQPVF FGWGKPLH FGWGKAIF FGWGKAIF FGWGKAIF FGWGKAIF	EEVRUCCTVN DSQRPSTLSH EEVRNICLTVN TKSRPSLMVH 0 45 	SRSEN- VVNIR-KNLE ARSEN- MMN-LRERTK 0 460 SCKFILVPT FCNLTLVPT -DLLISFYUQ -LDLISFYUQ -LDLISFYUQ -UDLISFYUQ -NVGIIGAPPA IPGVISFVPP IRGMISYSIA IPGVASFVIP IRGMISYSIA	PPLPTGYTGN PSLGEVSLGN PSLGEVSLGN LALENDVSGN 0 47 QCGSG-IEAW PCDTG-IEAW PCDTG-IEAW HKN-NTEDGI HKN-NTEDGI HKN-NTEDGI HKN-NTEDGI FKNRKGEKGI FMNRKGEKGI FMNRKGEKGI FKNRKGEKGI	AFAFVALT INWGTVAHHF AFAIFAAVT FFIVVNAESK 0.480 VNLEEEKNAM VNLEEEKNAM VNLEEEKNAM VNLEEEKNAM VNLEEEKNAM VNLCLFSA LVPMCLFSSA VTVDCLFSA VTVDCLFPTA ALSCCLPPPA LVPLCLPPTA	AGK	CQNPLGYALE EGLELSKLVS CONFPLGFALE TESLGSACGE) SO ASPKTLI ASPKTLI ASPKTLI TIQ-EPKEDI ITT-GT ASPNPRISIA FA SLQVKQVVDA SLQVIQVLDK LLKAGKTIDLG	LUREAKABUT LLRQSFKIN LIREAKREVT IISEVAKVDD 0 51 	EDYNKSVAD- KDYIKELIMG EEYNHSVAD- ARVVSSNVLN 0
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Figure 5. (**A**) Alignment of the deduced *FcAAT1* full length amino acid sequence with AATs from other sources. Gaps are indicated by dashes, letters with black background are identical amino acids, and letters with gray background are similar amino acids. The three motifs which are characteristic of most AATs are indicated: LALYYPLSGR, HKLID (related to the catalytic activity and conserved within the BAHD acyltransferase family) and DFGWG (highly conserved within the BAHD protein family and apparently required for conformation integrity of the protein structure). Sequences correspond to GenBank data library accession numbers: Cm (*Cucumis melo*), AAT1 (CAA94432), AAT2 (AAL77060), AAT3 (AAW51125), AAT4 (AAW51126); Cb (*Clarkia breweri*), BEBT (AAN09796), BEAT (AAF04787); Fa (*Fragaria ananassa*), AAT (AAG13130); Fc (*Fragaria chiloensis*), AAT1 (FJ548610); Fv (*Fragaria vesca*), AAT (AAN07090); Md (*Malus domestica*), AAT2 (AAS79797); Mp (*Malus pumila*), AAT1 (AAU14879); Ms (*Musa sapientum*), AAT1 (CAC09063); *Pc (Pyrus comunis*), AAT1 (AAS48090); Rh (*Rosa hybrida*), AAT (AAW31948); Vp (*Vasconcellea pubescens*), AAT1 (FJ548611). Sequences were aligned using Bioedit Sequence Alignment Editor v 7.0. (**B**) Phylogenetic analysis of *FchAAT1*. The phylogenetic tree built using MEGA software (version 3.1; http://www.megasoftware.net). Numbers on branches indicate bootstrap values (as a percentage). Sequences are the same used in panel **A** (see above).



Figure 6. DNA gel-blot analysis of genomic DNA from *F. chiloensis*. Genomic DNA (20 μ g per lane) was digested with the indicated restriction enzymes and hybridized with the corresponding ³²P-labeled specific probe for 3' UTR *FcAAT1*. Hybridization and stringency conditions as described in Materials and Methods.

A prospective analysis of four wild strawberry accessions (*F. virginiana* 'W9'; *F. vesca* ssp. vesca 'Geising'; *F. vesca* ssp. vesca f. alba; *F. moschata* 'Cotta') in comparison to *F.* × ananassa cv. Elsanta, described that wild accessions had higher aroma intensities than the cultivated one (16). The study showed that *F. virginiana* contains 15 times higher volatiles content than *F.* × ananassa. The aroma profile of wild species varied qualitatively and quantitatively, however the pattern shares similarities with the aroma profile of *F. chiloensis* fruit, especially related to ester compounds. Coincidently, alcohols which are predominant in *F. chiloensis* and accumulates as fruit ripening progresses, showed the same pattern in wild strawberries (16).

During ripening of F. chiloensis fruit there was a clear increase in the total content of volatiles, both esters and alcohols. As the production of esters increases, a clear increment of both AAT activity and transcript accumulation of FcAAT1 gene was observed. A good correlation was found between AAT activity and the total content of esters, especially with acetates and hexanoates. Esters from group 1, which includes the major esters produced by F. chiloensis's fruit, displayed a similar production profile during development as AAT activity, and therefore it can be suggested that AAT may have a significant role in the production of these important esters. Our findings are coincident with those reported by Perez et al. (20), who observed a high correlation between AAT activity and aroma profile during ripening in four cultivars of $F. \times$ ananassa. Also with Aharoni et al. (21) that reported that the expression of AAT increases during ripening of F. \times ananassa, peaking at the full red stage with high levels of transcripts. A good correlation was observed between *FcAAT1* transcript accumulation, AAT enzyme activity and ester production by the fruit, similarly to the findings of Carbone et al. (40) in $F. \times$ ananassa. Although FcAAT1 gene could perfectly explained the production of esters from group 1,



Figure 7. (**A**) Changes in *FcAAT1* mRNA abundance during development of the Chilean strawberry fruit by qPCR. The expression data corresponded to means of three replicates, normalized against *FcGAPDH1* abundance, using C1 stage fruit as calibrator, and expressed in arbitrary units \pm SE. Different letters indicate differences between stages (*P* = 0.05). (**B**) Changes in *FcAAT1* mRNA abundance in other tissues. Expression analysis of *FcAAT1* by qPCR was performed in leaves, flowers, runners and stem. The expression data are means of three replicates, normalized to *FcGAPDH1* abundance, using C1 stage fruit as calibrator and expressed in arbitrary units \pm SE. Different letters indicate differences between tissues (*P* = 0.05).

other AATs expressed at different development times should exist in order to explain the production of the remaining esters produced by the Chilean strawberry fruit.

Due to the high correlation between ester production and AAT activity we decided to isolate an AAT gene from F. chiloensis fruit (FcAAT1). This gene shows the nineteen amino acid residues that are absolutely conserved in the three conserved motifs which are characteristic of most AATs previously isolated from different fruit species. The first one is the less conserved motif, and it is located close to the N-terminus as previously described (21). The second motif, the most conserved within the BAHD acyltransferase family, is located in the middle of the sequence and it is involved in the catalytic mechanism (41). The last motif is also highly conserved within the BAHD protein family and is located in the C-terminus. Apparently, this last motif plays a structural function keeping the conformational integrity of the enzyme structure (42). Phylogenetic analysis reproduces the three subgroups previously described (42) and concludes that FcAAT1 belongs to subgroup II, which comprises the sequences from Fragaria AAT genus and Rosa hybrida.

In melon fruit, AATs are encoded by a multigene family of at least four members (42) suggesting that AAT genes could be part of a small multigene family. DNA gel-blot analysis for AAT gene in *F. chiloensis* (Figure 6) confirms this hypothesis, as it indicates that at least two gene copies exists according to *Bam*HI digestion

pattern which shows two fragments over 9 kb. Moreover, the digestion pattern of EcoRI shows five hybridization fragments between 2.3 kb and 9.4 kb. These two enzymes do not have restriction sites on the cDNA sequence of *FcAAT1* gene. On the other hand, the 3' end of the gene (that is recognized by the probe) is highly variable (Figure 5A), and therefore it is probable that these hybridization bands could represent other AAT gene family members present in the F. chiloensis genome. As far as we know, this is the first report that shows that the genomic organization of an AAT gene in strawberry genome is representative of a small multigene family. Other strawberry ripening-related genes, like those related to cell wall degradation such as endoglucanase, pectin methyl esterase, pectate lyase and polygalacturonase, show complex hybridization profiles indicating that they belong to large multigene families (23, 43). Certainly, the octoploid condition of strawberries (F. \times ananassa and F. chiloensis) is not directly related to the size of a determined gene family.

Transcript accumulation of FcAATI increased at the same time as fruit development. FcAATI is mainly expressed in fruit tissues, during the late stages of development and ripening, although there is some transcript accumulation in vegetative tissues at a similar expression level to that observed in small fruit. The strong induction of FcAATI at C3 and C4 stages strongly suggests a participation in ester formation, as it has been previously described for other AATs from a wide range of fruit species. However, the study of the kinetic parameters of FcAAT1 recombinant protein will provide more information about the real role and substrate specificity of this candidate gene.

In conclusion, our study reveals an increment in AAT activity which is related to an increment in ester production during ripening of the Chilean strawberry fruit. In addition, *FcAAT1* gene is highly expressed in fruit tissue during ripening of *F. chiloensis* and it could be responsible for the production of important esters related to aroma.

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