

VpAAT1, a Gene Encoding an Alcohol Acyltransferase, Is Involved in Ester Biosynthesis during Ripening of Mountain Papaya Fruit

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Mountain papaya (*Vasconcellea pubescens*) is a climacteric fruit that develops a strong and characteristic aroma during ripening. Esters are the main volatile compounds produced by the fruit, and most of them are dependent on ethylene. As esters are synthesized through alcohol acyltransferases (AAT), a full-length cDNA (*VpAAT1*) was isolated that displayed the characteristic motifs of most plant acyltransferases. The full-length cDNA sequence was cloned and expressed in yeasts, obtaining a functional enzyme with high AAT activity toward the formation of benzyl acetate. The transcript accumulation pattern provided by qPCR analysis showed that the *VpAAT1* gene is expressed exclusively in fruit tissues and that a high level of transcripts is accumulated during ripening. The increase in *VpAAT1* transcripts in fruit is coincident with the increase in AAT activity; transcript accumulation is induced by ethylene, and it is avoided by 1-methylcyclopropene (1-MCP) treatment. The data indicate that *VpAAT1* is involved in aroma formation and that ethylene plays a major role in regulating its expression.

KEYWORDS: Alcohol acyltransferase; aroma; ester production; fruit ripening; 1-methylcyclopropene; *Vasconcellea pubescens*

INTRODUCTION

Mountain or highland papaya (Vasconcellea pubescens) is a diploid (2n = 18) dicotyledoneous species. It is native to the Andean regions of South America and belongs to the Caricaceae family, which includes the *Carica* and *Vasconcellea* genera (1, 2). The fruit is climacteric and exhibits a characteristic rise in ethylene production during ripening, accompanied by softening, changes in color, and development of a strong and characteristic aroma (3-5). The main volatile compounds produced by the fruit are esters and alcohols (4). Most of the esters found in mountain papaya fruit are potent odor compounds, and the dynamic of their production during ripening has been previously reported (4). In addition, the treatment of mountain papaya fruit with 1-methylcyclopropene (1-MCP), a strong inhibitor of ethylene action (6), has been shown to inhibit ethylene production and the production of aroma volatile compounds in mountain papaya fruit, particularly esters (4). Thus, most esters identified in mountain papaya displayed a clear modulation by ethylene.

Esters are produced from alcohols and acyl-CoAs through the action of alcohol acyltransferases (AAT) (7). Plants contain large families of AATs, with about 61 putative members in

Arabidopsis (8). AAT activity is responsible for the production of esters, and it has been measured in two main plant tissues: flowers and fruits (9). During the past few years, several AAT genes have been isolated and characterized from several fruit species, such as strawberry (9, 10), melon (11, 12), apple (13, 14), banana (7), grape (15), and apricot (16). According to their sequences, acyltransferases dependent on coenzyme A (CoA) have been included within a wide and divergent family of proteins, the BAHD superfamily (17). Among them the HXXXD motif, located in the middle of the protein sequence, is highly conserved in superior plants and yeasts. The substitution of the histidine residue from this motif causes the loss of protein function (18), which suggests that it could be involved in the transfer of the acyl group from acyl-CoA toward an alcohol. Another highly conserved motif in higher plants in this superfamily is the DFGWG sequence, located near the carboxylic end of the protein, which seems to be involved in the maintenance of the structural integrity of the enzyme (19).

An important question in the field has been the identification of enzymes that are critical for production of the distinctive blend of esters characteristic of each fruit species (13). The available information indicates that substrate specificity of AAT enzymes seems to be wide but with differential preferences toward acyl-CoAs and alcohols. This could indicate that the particular aroma

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of each fruit or flower depends on the interaction of different types of AATs, each one with preferential, although nonexclusive, substrates. In addition, AAT sequences provide valuable information about enzyme properties, although in some cases it has been difficult to predict substrate selectivity, and minor differences in the amino acid sequence could alter the ability of a certain enzyme to produce some esters (7, 11, 12). On the other hand, substrate availability for AAT enzymes is also another aspect to consider.

In the present paper, the isolation and characterization of an AAT gene for the first time from the Caricaceae family was performed. In addition, it was demonstrated that the encoding protein is functional and active toward several substrates, and the role of ethylene on the expression of the gene was investigated.

MATERIALS AND METHODS

Plant Material. Mountain papaya (*V. pubescens*) fruit and other vegetative tissues were collected in February 2005 from orchards located at Lipimavida (34° 51′ S; 72° 08′ W; 20 m asl), on the coast of Curicó, Chile. Young expanding fruit was picked and staged as small green fruit (SGF), medium green fruit (MGF), or large green fruit (LGF), according to the guidelines of Gaete-Eastman et al. (5). Ripening fruit was harvested after the first signs of chlorophyll breakdown, sorted for size and then randomly divided into three lots: one lot was left intact (control fruit); the second lot was treated with 1-MCP; and the last one was treated with ethylene (Ethrel), both on the same day of harvest (day 0). After each treatment, the fruit was allowed to ripen at 20 °C in separate rooms.

1-MCP and Ethylene Treatments. Fruit was placed inside an airtight chamber of 0.28 m³ and treated with 0.3 μ L L⁻¹ 1-MCP for 16 h at 20 °C. One hundred and fifty milligrams of EthylBloc (0.14% 1-MCP) was dissolved in 20 mL of 0.9% (w/v) sodium hydroxide to allow the release of 1-MCP gas. The chamber was immediately closed after EthylBloc application, and it was opened only after 16 h to remove the 1-MCP-treated fruit, which was subsequently left at 20 °C. For ethylene treatment, the fruit was dipped during 5 min in 25 L of an aqueous solution of 2 g L⁻¹ Ethrel 48 SL (Bayer CropScience S.A.; ethephon, 2-chloroethyl phosphonic acid), allowed to dry at room temperature, and then left at 20 °C in separate rooms.

Sampling of fruit from each treatment (ethylene, 1-MCP, and nontreated) was performed every 2 days (starting on day 1) until completing 13 days at 20 °C. Three replicates of four fruits were randomly selected and assessed for volatiles and ethylene (4). In addition, on each sampling date, pulp tissue from each fruit was immediately frozen in liquid nitrogen and stored at -80 °C until required.

Ethylene Production Rate. The procedure employed was described previously (4). Briefly, the fruit was introduced into airtight respiration chambers (6 L), and after 3 h of incubation at 20 °C, 1 mL gas samples were withdrawn from the headspace and quantified for ethylene in a Perkin-Elmer (Clarus 500) gas chromatograph. Three independent ethylene samples were taken per chamber, and results were expressed as means \pm standard error (SE) (μ L kg¹⁻ h⁻¹).

Isolation of VpAAT1 Gene from V. pubescens. To isolate the AAT gene, total RNA (1 μ g) was extracted from 6 g of pulp tissue of a ripe mountain papaya fruit (day 5 of storage) using an adapted version of the CTAB method (20). Then the RNA was treated with DNase I amplification grade (Invitrogen) and cDNA synthesized using a BD SMART PCR (Clontech) kit according to the manufacturer's instructions. Degenerate primers (VpAAT1 F = 5'-TACTAYCCHYTHKCYGGAAG-3' and VpAAT1deg R = 5'-GBCYKYCCCCATCCAAA-3') were designed to match AATs conserved regions. PCR runs were performed, and PCR product was cloned onto pCR 2.1 TOPO (Invitrogen) and manually sequenced through ALFexpress II (Amersham Biosciences) using a thermosequenase dye terminator kit (Amersham Biosciences). To complete the gene sequence, specific internal primers were designed for 5' and 3' RACE-PCR on the basis of the isolated sequence (VpAAT1RACE F = 5'-TCCATTGGCCGGACGTCTCAGGG-3; VpAAT1RACE R = 5'-ATGGCAGCCATCT CACTGGGACC-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 by Macrogen Inc. (Seoul, Korea). The full-length cDNA sequence was amplified by using primers specially designed to match the initial and final transcription zones of the gene (Vp-AAT1 F = 5'-ATGGCAGAGAAAGCTAGTTC-3'; Vp-AAT1 R = 5'-AATGGCGGACACAATAAAGA-3') and then sequenced.

The nucleotide and deduced amino acid sequences were analyzed using Vector NTI Advance 9.0 software (Invitrogen, 2003). The similarity analysis was 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 (21). The multiple alignment of amino acid sequences was performed using the software BioEdit Sequence Alignment Editor v7.0 (22). The phylogenetic tree was built using MEGA software (version 4; http://www.megasoftware.net) (23) using the maximum parsimony method and Bootstrap analysis (1000 replicates).

DNA Gel-Blot Analysis. Mountain papaya genomic DNA was extracted from a pool of young leaves (2 g) as described by Murray and Thompson (24). Probe for DNA gel-blot analysis of VpAAT1 was designed from the 3'-end portion of the ORF sequence. The 108 bp probe (from position 1308 to 1415 in VpAAT1 sequence) was prepared through PCR reaction with the primers QAAT1-F (5'-AGGAGAGAAAGG-GATCGTAG-3') and QAAT1-R (5'-TCAGCGGAAACAAGTAG-TTG-3'), and radiolabeled using $[\alpha^{-32}P]dCTP$ (Easytides, NEN Life Sciences Products). For Southern blots, 20 μ g of genomic DNA was digested with BamHI, HindIII, EcoRV, and EcoRI, fractioned on a 0.7% agarose gel, and transferred to Hybond-N+ membranes (Amersham Biosciences) using 20× SSC as blotting buffer. Membranes were prehybridized at 42 °C for 4 h in a solution containing 50% deionized formamide, 1% (w/v) 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 with $2 \times$ SSC containing 0.1% (w/v) SDS for 15 min at 42 °C, followed by three washes with 1× SSC plus 0.1% (w/v) SDS during 15 min at 50 °C. The blots were exposed, and autoradiograms were scanned in a densitometer (FLA-5100 Imaging System, Fujifilm, Japan).

Real-Time (qPCR) Expression Analysis. Total RNA was extracted from 6 g of mountain papaya fruit pulp (control, 1-MCP and ethylenetreated papaya fruits) after 1, 3, 5, 7, 9, and 13 days at 20 °C using an adapted version of the CTAB method (20). In addition, total RNA was also extracted from other vegetative tissues: flower, leaf, root, and stem. Total RNA was treated with DNase I amplification grade (Invitrogen) and cleaned using the RNeasy Plant Mini Kit (Qiagen, Germany). 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 sampling date were employed. Specific primers for a divergent 3'-end region of VpAAT1 and the α -elongation factor 1 (*VpEF1*- α ; as internal control) genes were designed using Vector NTI v9, with high stringency to avoid amplification of nonspecific PCR products. Primers were tested by RT-PCR and the amplification products sequenced to ensure their specificity. Primer pair sequences were QAAT1-F and QAAT1-R (described above) and EF1-F (5'-TCAATGAACCCAAGAGGCCATCC-3') and EF1-R (5'-CACG-TCCCAC TGGAACAGTTCCA-3').

The amplicon sizes were 108 bp for the AAT gene and 96 bp for $VpEF1-\alpha$. The amplification reactions were performed using Brilliant SYBR Green QPCR Master Mix (Stratagene) according to 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 for 20 s; melting curve from 58 to 95 °C at 0.5 °C increments. A dilution series was built to estimate the amplification efficiency using a cDNA mix as template prepared from control fruit samples (1-13 days of storage). Each reaction was performed in triplicate, and a negative water control was included in each run. Fluorescence was measured at the end of each annealing 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 $VpEF1-\alpha$ gene and using nontreated fruit samples from day 1 as calibrator, with a nominal value of 1. The method described by Pfaffl (25) was used to make all calculations.

Expression of Recombinant VpAAT1. The full-length sequence of VpAAT1 was initially cloned into *Escherichia coli* TOP 10 One Shot (Invitrogen) to select colonies with the right orientation. The insert was then cloned in the pYES2.1 TOPO-TA cloning vector following the instructions provided by the manufacturer (Invitrogen). The construct was used to transform the *Saccharomyces cerevisiae* cell line INVSc1. Transformed yeasts were grown at 30 °C in selective medium (SC-U) with 2% galactose as inducer of the recombinant protein expression, with constant stirring and bubbling of sterile air until the OD₆₀₀ of the culture reached <1 U.

Purification of Recombinant VpAAT1. The purification of the recombinant protein was carried out according to the method of El-Sharkawy et al. (11) with some modifications. Six flasks containing 100 mL of yeast culture induced with galactose (OD₆₀₀ of 0.8) were centrifuged (1800g for 5 min at room temperature), and the cells collected from each flask were resuspended in 2 mL of buffer A (50 mM sodium phosphate (pH 7.5), 10% (v/v) glycerol, 0.3 M NaCl) containing 2 mM β -mercaptoethanol. The cells were mechanically ground in liquid nitrogen for 10 min and stored at -80 °C until needed. To extract AAT enzyme, the powder was thawed and centrifuged at 10000g for 20 min at 4 °C. The crude extract obtained was purified through a BD Talon Metal Affinity column (BD Biosciences), an affinity column designed to purify polyhistidine-tagged proteins, according to the manufacturer's protocol. The recombinant protein was eluted with buffer A containing 150 mM imidazole. Proteins were quantified according to the Bradford method (26) and visualized through 10% SDS-PAGE gels.

Assay of AAT Activity. AAT activity of recombinant VpAAT1 protein was quantified by its ability to convert alcohols and acyl-CoAs into the corresponding ester (10, 27). AAT activity was assayed in 500 μ L of total volume in the presence of 2 mM alcohol-250 μ M acyl-CoA in 50 mM Tris-HCl (pH 7.5) buffer containing 10% (v/v) glycerol and 1 mM dithiothreitol (DTT) (12). A set of three acyl-CoAs (acetyl-, butanoyl-, and hexanoyl-CoA) and nine different alcohols were assayed: ethanol, methanol, butanol, hexanol, octanol, benzyl alcohol, geranyl alcohol, 1-phenylethanol, and cinnamyl alcohol. Each reaction assay contains the mixture of one alcohol and one acyl-CoA per time. The reaction was initiated by the addition of 200 μ L of purified protein (10-15 μ g), and the mixture was incubated at 30 °C for 2.5 h in sealed Eppendorf tubes. 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 0.5 μ L of 1,2-dichlorobenzene as internal control. 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 each ester was done by a gas chromatograph fitted with a flame ionization detector (GC-FID) (Perkin-Elmer, Clarus 500) (4). The separation and quantification of each ester was done by a GC-FID following the procedure described by Balbontín et al. (4). A calibration curve was prepared for each ester. AAT enzyme activity was expressed as picokatals (pmol s⁻¹) per milligram of protein. Protein content was determined using BSA as standard (26). Determinations were performed in triplicate and expressed as mean \pm SE.

AAT activity was also assayed in mountain papaya pulp samples obtained during ripening at 20 °C. Frozen pulp 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 buffer 100 mM Tris-HCl (pH 8)-1 M KCl, 0.1% (v/v) Triton X-100, containing 1 mM phenylmethanesulfonyl fluoride (PMSF) and 2 μ M leupeptin as protease inhibitors. The mixture was stirred for 20 min at 4 °C, filtered through Miracloth, and centrifuged (10000g for 20 min). The supernatant was desalted through a Sephadex G-25 gel filtration column (PD-10 Pharmacia) in the presence of 50 mM Tris-HCl (pH 7.5) buffer containing 10% (v/v) glycerol and 0.5 mM DTT. AAT activity was quantified by its ability to convert acetyl-CoA and hexanol into hexyl acetate (10, 27). The reaction was performed as described above in the presence of 10 mM hexanol-490 µM acetyl-CoA-50 mM Tris-HCl (pH 7.5) buffer, 10% (v/v) glycerol, and 0.5 mM DTT. The reaction was initiated by the addition of 300 μ L of protein extract and the mixture incubated at 30 °C for 2 h. A calibration curve was prepared with hexyl acetate.

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).

RESULTS

VpAAT1 Shares High Similarity with AATs from the BAHD Family. With the aim to isolate ripening-related AAT genes from mountain papaya fruit, degenerate primers were designed on the basis of two conserved regions in the BAHD superfamily gene sequences: the motif YYPLAGRL, located close to the N-terminal, and the DFGWGR motif, at the C-terminal end (9). By PCR a fragment of 1200 bp was amplified with high homology to other AAT sequences, which was used as a template to design internal primers for 5' and 3' RACE-PCR runs. Two fragments of 1300 and 800 bp were obtained using these primers. A composite cDNA sequence of 1622 bp called *VpAAT1* (GeneBank accession no. FJ548611) was generated from all fragments.

Analysis of the VpAAT1 sequence revealed an ORF of 1383 bp and a deduced amino acid sequence of 463 amino acids with a molecular weight of 51.4 kDa (Figure 1A). The sequence also contains 60 and 173 bp of 5'- and 3'-UTR, respectively. VpAAT1 shares the characteristic motifs found in other plant acyltransferases, including the active site motif HXXXDG (amino acids 166–171). In *VpAAT1* the His and Asp residues are conserved; however, the Gly is replaced by Ala. Some AATs also have Ala in this position, but it is not known if this change could affect the activity or substrate preferences (13). There is also another highly conserved motif located toward the carboxylic end formed by five amino acids, DFGWG (amino acids 381-385). VpAAT1 also exhibits a third less conserved motif, LXXyyplaGR (amino acids 75-84), located near the amino-terminal end, which is common among AATs involved in the synthesis of volatile compounds in fruits and flowers. Finally, it is important to highlight the presence of Thr in position 266, which has been shown to be essential for enzyme activity (12).

Sequence Comparison and Phylogenic Analysis. The VpAAT1 deduced amino acid sequence was aligned and compared with 15 plant acyltransferases (Figure 1A). The highest similarity was found between VpAAT1 and CmAAT3 isolated from Cucumis melo (12) and BEBT (benzoyl coenzymeA: benzyl alcohol benzoyl transferase) isolated from *Clarkia breweri* (28), with 67 and 61% identity at the amino acid level, respectively. A phylogenic tree was built from the previous multiple alignment, and the grouping pattern provides three main subgroups (Figure 1B). VpAAT1 was clustered into subgroup III with AATs related to the synthesis of esters in melon and Clarkia (CmAAT3 and CbBEBT). The same cluster also incorporates AATs isolated from apple (MpAAT1), pear (PcAAT1), banana (MsAAT1) (7), and melon (CmAAT1 and CmAAT2) (11). Subgroup II comprises AATs isolated from rose (29) and different strawberry species, such as *Fragaria* \times *ananassa* (9), *Fragaria* vesca (7), and Fragaria chiloensis (10); finally, subgroup I was formed only by Cm-AAT4 from melon (12).

DNA Gel-Blot Analysis. To analyze the complexity of mountain papaya's AAT family, genomic analysis was performed using DNA gel blots. By using a probe that matches the 3' end of the coding sequence of the *VpAAT1* gene (Figure 1A), a divergent region of AAT single-hybridization fragments were detected in DNA digested with *Hin*dIII, *Eco*RV, and *Eco*RI enzymes, all of them ranging between 2.3 and 9.4 kb. Only *Eco*RI has a restriction site at nucleotide 403 of the *VpAAT1* sequence. Analysis of *Bam*HI-digested DNA revealed two hybridizing bands around 9.4 kb and over 6.6 kb (Figure 2). Considering that no restriction sites for *Bam*HI are included in the coding sequence, its restriction pattern could suggest two possibilities according to the location Article A)

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VPAAT1	-MAEKASSLM	FNARRHEPEL	ITE-ARPTPR	BIKLLSDIDD	QDGLRFQVPI	IQFYKNNS	S-MQGKNPAK	IIKSALAET	VHYYPLACEL	REGFGRKL	MVECTGECIL	FISADADVTL	HEFGDDLPPP	FPCLV-ELLY	DVPGSSGIID
FCAAT1	MEK	IEVSIISKYT	IKE-SSSL	LQPYKLSLLD	QLTPPAYVPM	VFFYPITE	HVFNLPQTLA	DLRQSLSET	ALYYPLSCE-	VKNNL	YIDNFEECVP	YLEAQVNCDM	TDFLRLGKIE	CLNEFVSIKP	FSMEAISDER
FVAAT	MEK	IEWSIISKHT	IKE-STSSSP	LQPYKLTLLD	QLTPPSYVPM	VFFYPITG	PAVFNLQTLA	DLRHALSET	TLYYPLSCH-	VKNNL	YIDDFEECVP	YLEARVNCDM	NDFLRLPKIE	CLNEFVPIKP	FSMEAISDER
FAAAT	MEK	IEWSINSKHT	IKE-STSSTP	LQPYKLTLLD	QLTPPAYVPI	VFFYPITD	HDFNLPQTLA	DLRQALSET	TLYYPLSCH-	VKNNL	YIDDFEECVP	YLEARVNCDM	TDFLRLRKIE	CLNEFVPIKP	FSMEAISDER
MpAAT1	-MMSFSV	LOWKRLOPEL	ITE-AKSTPO	ETKFLSDIDD	QESLRVQIPI	IMCYKDNP	SLNKNRNPVK	AIREALSRA	VYYYPLACEL	REGP NRKL	VVDCNGECIL	FVDASADVTL	EQLGDKILPP	CPLLE-EFLY	NFPGSDGIID
MdAAT2	-MMPFSV	LOWKRLOLEL	ITE-AKPTLO	EAKFLSDIDD	QEGLRFQVPV	IMCYKDNP	SLNKNCNPVK	VIREALSRA	VYYYPLAGEL	KEGP NRKL	MVDCNGECIL	FVDASADVTL	EQLGDKILPP	CPLLE-EFLF	NFPGSDGIIG
PCAAT1	-MMSLSV	LOWKRLOPEL	ITE-AKPTPO	ETKFLSDIDD	QEGLRFQLPV	IMCYKDNP	SLNKNRNPIK	VIKEALSRA	VYYYPLAGEL	REGP NRKL	MVNCNGECIL	FVEASADVTL	EQLGDKILPP	CPLLE-EFLF	NFPGSDGIIG
RhAAT	MEK	IEVSIISRDT	IKE-SAASSS	LHPYKLSIID	OFTPTTYFPV	IFFYPITD	RVFNLPOTLT	DLKNTVSOA	TLYHPLSCS-	IKNNL	YIDDFEACIP	YLOARVNFHM	IDFLRLPKIE	WLNEFVPMAP	YRKETIS-EF
MRAAT1	MS	FAWTRTSRSL	VTR-COVTPT	GSLGLSAIDR	VPGLRHMVRS	LHVFR	OGREPAR	TIREALSKA	VKYYPFACEF	VDDPEGGGEV	RVACTGECAW	FURAKADCSL	EDVKYLDLP-	-LMIPEDALL	PEPCPGLNPL
CmbaT1	DES	PHARKCOPEL.	TAE-ANPTPY	REKOLSDUDD.	OOST.PLOT.PF	UNTVPHNP	S-LEGEDPVK	VIKEATORA	VEVVPLACET.	REGP GREL	FURCTORETL	PTRADADVSL.	REFWOTLPVS.	LSSMONNTTH	NALNSDEVIN
CmaaT2	METMOTTOPS	POMPECOPPT.	TAR-ANDTRY	FFFOT COVOD	OOST.PROT.PT.	WNT VWWND	G-LEGEDRUY	UTVENTAVA	UPWYDT ACHT	PEGP GPFT.	PURCTORATI.	PTUADADVCT.	POPPDTI.DVC	LCOMPNETTU	MELNEDOVIN
Calatz	-WAG	POLORCOPOL	TON COOTON	EFFOL COTOD	OPOLEROTEU	TORVENDE	D-MACTODAD	UTVPATAVA	UPPUNDAN	BROD OPET	PUPCTOPAIN	PTUNDADUCT	ROPODALODD	PROTE PRTP	DUDMOCOULD
CHARTS	-100004	PUTURAUFUL	THEODEDDU	LODINICIID	QEODERVITY	I PUDUNNOV	CHODIDINATA	VINEALANA	CONTRACTOR	ABOFGAAD	PVBCIGES VA	PLOADADVSL	EQFORALQFF BDTI VBDIDIP	FFCDB-BFDF	LICHTERDIER
CILARIA		MENAVLSKET	TIPSSPIPPH	LOPENLSELD	QUSPRLITPL	LEP IPAKKSI	QUQUNARATA	THATSUSAT	SKFILLAGS-	11G-K	STHUNDREAV	PRIMATINSNA	PDILKEPNNE	VEINLEPCS-	LUCNIKPIES
CDBEBI	-MARDQ-SLS	FERCERAPEL	ING-ANUIPH	FLEEDARD	QEGERFQIPV	IQPIKANA	ESNQERDPVQ	VIREGIARA	VIIIPPACISL	REVDGRAL	VVECTGEEVM	PIDADADVIL	EQFGDALQPP	PPCFD-QLLP	DVPGSGGILD
CDBEAT		MNWTMHSKKL	LKESIPTPNH	LOKLNLSELD	QIQIPFYVGL	IFHYETLS	DNSDITLS	KLESSLSET	TLYYHVAGEY	NGTDC	VIECNDOUIG	YVETAFDVEL	HQFLLGEESN	NLDLLVGLSG	FLSETET
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VPAAT1	TPLLLIOVTR	LKCEGFIFAL	RLNITMSEAS	GLVOEMTAVG	EMARGORS	LSIQPV	WERHLLNARD	PPRVTHIHHE	YDDLEDTKG-	TIIPLDDM	VHRSFFFGPS	EMAAIRRLVP	AHF	-HRSTT-SEV	LTAYLWRCYT
FCAAT1	YPLLGVOVNV	FDSC-IAIGV	SLSHKLINGR	TAYCELKSWG	AVFEGCR		-EDVIHPSLS	EAALLFPPRD	DLPEKYADQM	EGLWFAGKKV	ATRRFVFGAK	AISSIQDEAK	SES	-VPKPSRVQA	VTGFLWKHLI
FVAAT	YPLLGVOVNI	FNSC-IAIGV	SVSHKLINGR	TSDCGLKSWC	AVFOGSR		-DKIIHPNLS	QAALLFPPRD	DLPEKYARQM	EGLWFVGKKV	ATRRFVFGAK	AISVIQDEAK	SES	-VPKPSRVQA	VISFLWKHLI
FAAAT	YPLLGVOVNV	FDSC-IAIGV	SVSEKLIDGG	TADCELKSWG	AVFRGCR		-ENIIHPSLS	EAALLFPPRE	DLPEKYVDQM	BALWFAGKKV	ATRRFVFGVK	AISSIQDEAK	SES	-VPKPSRVHA	VTGFLWKHLI
MpAAT1	CPLLLIOVIC	LTCEGFILAL	RLNHTMOLAA	GLLLGLTAIA	EMADGAHA	PSILPV	WERELLFARD	PPRITCAHHE	YEDVIGHSDG	SYASSNOSNM	VQRSFYFGAK	EMRVLRKQIP	PHL	-ISTCSTFDL	ITACLWKCRT
MdAAT2	CPLLLVOVTC	LTCEGFILAL	RVNETMOLAP	GLLLELTAIA	EMAEGAHA	PSILPV	WERELLFSRD	PPRITCAHHE	YEDVIDHSDG	LYASSNOSNM	VORSFYFGAK	EMRVLRKQIP	PHL	-ISTCETFDL	ITACLWKCRT
PCAAT1	CPLLLVOVTC	LTCEGFILAL	RUNITICEAT	GLLMELTAIT	ENGEGADA	PSILPV	WERELLFARD	PPRITCAHYE	YEDVIDHSDG	SYAFSNOSNM	VORSFYFGAK	EMRVLRKQIP	PHL	-ISTCETFDL	ITACLWKCRT
RhAAT	LPLLGIOVNI	FDSE-IAIGV	SESIKINGO	TASOSLKSWV	AIFOGYR		-NKIIHPNLS	OAALLLPSRD	DLPEKYVAM	ERMWFGEKKV	VTRREVEDAK	AISALODEGK	SEY	-VPKPSRVOA	LTGFLWKHOL
MaAAT1	DLPLMLOVTE	FVGeGFVVGL	ISVICTABLE	GVVOGINAVA	ETAUGLPK	PTVEPA	WSREVIP N	PPKLPPGGPP		VEPSEEL	LHATVDLSPD	HIDHVKSRHL	RLT	-GORCETFDV	ATANLWOSET
CmAAT1	SPLLLTOUTR	LECCOPTEGL.	CENECTMANCE	GIVODMENTA	FTARGAPA	PSTLPV	WORALLTARD	PPRITERHVE	VDOVUDMES-	GLT PUNSK	TDOLFFFSOL	OTSTLEOTLE	AHL	-HDCPS-FEV	LTAYWWRLPT
CmbbT2	GDLLL TOUTD	LECORTROT	HPDUTMANOP	GTACOMPATA	ETADOARA	POTLOU	WORAT.LTAPD	DEDTTUDUVE	VDOUVDTER-	TLTDANNM	TOPLEPETOR	OTSTL POTL P	AUT	-HDCCC. PRV	LAAVUMPLET
CmAAT2	CPLLLTOUTP	LECCOPTENT.	PT.NITTMOULC	GL.VODMANG	EMANGATA	DOUDDU	WORALLNAPD	PPRUTCHURP	VDEUUDTEG.	TTTPLDDM	AUDCEPEPODC	FTCATEVALD	GWT.	-ROCCE-VEV	LTACIMPEPT
CallTA	VROTUTIONIT	PROPATATOT.	CLIMPTICAN	TROOMEDOWN	TTALETTOT	UCCOMPANY	UNVYCRACI.S	DOTNET DENC	CI. THROUGH	DECCTEMPER	PRODEVEDCE	ATTOLYAYAY	COD	TONDECUPT	LECETWEVIN
Charac	CDITIT	THOROTALDL	DT MELTINA A A	OTUT PMYAUG	TINGEDUSUD	BOTT BU	WEDDUTINADU	POINDEPPRO	VERUEAT	TPTDEDOL	APORPERACT	FTCAMPYOTD	DWI	- DOCOMPTEN	LTLOUNDODT
COBEDI	DDIALTYIK	BROGOLUTON	OPHILITION	THOTOLOUN	ENGRATE-	Forney	BUNDARY	CI ADI MDCAR	ILEVAGI	PROVER	NEKOPPPOOL	STORARNYIF	PROCEDERE	-ROCOLLIDY	UTACLORACKI
CDDDAL	FFDAALBUAA	FREEDEVIOR	Or Mer Tolent	THOTOMANA	VUCTA		BYARFIF	GLAFLINFOAR	vuniffffo-	THEFE	VOLREVEREN	ALICURCEAL	PPROPADADA	KKKEBKYDD	VIAPBOROUL
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	310	0 32	0 33(34	0 350	36	0 37	0 38	10 39	0 40	410	42	0 43	44	0 45
	310	0 32 	0 33(34 <u> </u>	0 350 	36	0 37	0 38 	10 39 	0 40 	410	42 	0 43 	44 	0 45
VPAATI	310 IALQPDPE	32 EEMRVICVVN	330 SRTKLN-	34 PPLPTGFY	0 350 GIAFPAAISQ	36 AKKI	0 37 CENPFGYTLQ	0 38 LVKQTKVDVT	10 39 EEYMRSAAD-	0 40 	410 MAMKGRPHFT	42 VVRRY-MVBD	0 43 VTRAGFGLVD	44 FGWCRPEPVY	0 45 GGPAKGGVGP
VPAAT1 FCAAT1	310 IALQPDPE AASRALTSGT	32 EEMRVICVVN TSTRLSIAAQ	0 330 SRTKLN- AVNLRTRMNM	34 PPLPTGFYGN ETVLDNATGN	0 350 GIAFPAAISQ LIWWAQAILE	36 AKKI LSHTTPEI	0 37 CENPFGYTLQ SDLKLCDLVN	0 38 LVKQTKVDVT LLNGSVKQCN	0 39 EEYMRSAAD- GDYFETFKGK	0 40 EGYGRMCEYL	410 MAMKGRPHFT DFQRTMSSME	42 VVRRY-MVSD PAPDIYLFSS	0 43 VTRAGFGLVD WTNF-FNPLD	44 PGNGRPEPVY FGNGRTSW	0 45 GGPAKGGVGP IGVAGKIESA
VpAAT1 FcAAT1 FvAAT	310 IALQPDPE AASRALTSGT ATSRALTSGT	BEMRVICVVN TSTRLSIAAQ TSTRLSIATQ	SRTKLN- AVNLRTRMNM VVNIRSRRNM	34 PPLPTGFYGN ETVLDNATGN ETVWDNAIGN	GIAFPAAISQ LIWWAQAILE LIWFAPAILE	36 AKKI LSHTTPEI LSHTTLEI	0 37 CENPFGYTLQ SDLKLCDLVN SDLKLCDLVN	0 38 LVKQTKVDVT LLNGSVKQCN LLNGSVKQCN	10 39 EEYMRSAAD- GDYFETFKGK GDYFETFMGK	0 40 EGYGRMCEYL EGYGSMCEYL	410 MAMKGRPHFT DFQRTMSSME DFQRTMSSME	42 VVRRY-MVSD PAPDIYLFSS PAPEIYLFTS	0 43 VTRAGFGLVD WTNF-FNPLD WTNF-FNQLD	44 PGNGRPEPVY PGNGRTSW PGNGRTSW	0 45 GGPAKGGVGP IGVAGKIESA IGVAGKIESA
VpAAT1 FcAAT1 FvAAT FaAAT	310 IALQPDPE AASRALTSGT ATSRALTSGT AASRALTSGT	0 32 EEMRVICVVN TSTRLSIAAQ TSTRLSIAAQ TSTRLSIAAQ	0 330 SRTKLN- AVNLRTRMNM VVNIRSRRNM AVNLRTRMNM	94 PPLPTGFY ETVLDNATGN ETVWDNAIGN ETVLDNATGN	0 350 GIAFPAAISQ LIWWAQAILE LIWFAPAILE LFWWAQAILE	36 AKKI LSHTTPEI LSHTTPEI	0 37 CENPFGYTLQ SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN	0 38 LVKQTKVDVT LLNGSVKQCN LLNGSVKQCN LLNGSVKQCN	0 39 EEYMRSAAD- GDYFETFKGK GDYFETFMGK GDYFETFKGK	0 40 L EGYGRMCEYL EGYGSMCEYL EGYGRMCEYL	A10 MAMKGRPHFT DFQRTMSSME DFQRTMSSME DFQRTMSSME	42 VVRRY-MVSD PAPDIYLFSS PAPEIYLFTS PAPDIYLFSS	0 43 VTRAGFGLVD WTNF-FNPLD WTNF-FNQLD WTNF-FNPLD	44 FGWGRPEPVY FGWGRTSW FGWGRTSW FGWGRTSW	0 45 GGPAKGGVGP IGVAGKIESA IGVAGKIESA IGVAGKIESA
VpAAT1 FcAAT1 FvAAT FaAAT MpAAT1	31) IALQPDPE AASRALTSGT ATSRALTSGT AASRALTSGT LALNINPK	0 32 EEMRVICVVN TSTRLSIAAQ TSTRLSIAAQ TSTRLSIAAQ EAVRVSCIVN	0 330 SRTKLN- AVNLRTRMNM VVNIRSRRNM AVNLRTRMNM ARGKHNN	9 34 PPLPTGFYGN ETVLDNATGN ETVLDNAIGN ETVLDNATGN VRLPLGYYGN	0 350 GIAFPAAISQ LIWWAQAILE LIWFAPAILE LFWWAQAILE AFAFPAAISK	36 AKKI LSHTTPEI LSHTTPEI AEPL	0 37 CENPFGYTLQ SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN CKNPLGYALE	0 38 LVKQTKVDVT LLNGSVKQCN LLNGSVKQCN LLNGSVKQCN LVKKAKATNN	0 39 EEYMRSAAD- GDYPETFKGK GDYPETFKGK GDYPETFKGK EEYLRSVAD-	0 40 L EGYGRMCEYL EGYGSMCEYL EGYGRMCEYL L	410 MAMKGRPHFT DFQRTMSSME DFQRTMSSME DFQRTMSSME LVLRGRPQYS	42 VVRRY-MVSD PAPDIYLFSS PAPEIYLFTS PAPDIYLFSS STGSYLIVSD	0 43 VTRAGFGLVD WTNF-FNPLD WTNF-FNPLD WTNF-FNPLD NTRVGFGDVN	44 FGNGRPEPVY FGNG RTSW FGNG RTSW FGNG RTSW FGNG QPVF	0 45 GGPAKGGVGP IGVAGKIESA IGVAGKIESA IGVAGKIESA AGPVKA
УрААТ1 РсААТ1 Р∨ААТ РаААТ МрААТ1 МДААТ2	31(IALQPDPE AASRALTSGT ATSRALTSGT AASRALTSGT LALNINPK LALNINPK	0 32 EEMRVICVVN TSTRLSIAAQ TSTRLSIAAQ TSTRLSIAAQ EAVRVSCIVN EAVRVSCIVN	0 330 SRTKLN- AVNLRTRMMM VVNIRSRRMM AVNLRTRMMM ARGKHNN ARGKHNN	94 PPLPTGFYGN ETVLDNATGN ETVLDNATGN ETVLDNATGN VRLPLGYYGN VRLPLGYYGN	GIAFPAAISQ LIWWAQAILE LIWFAPAILE LFWWAQAILE AFAFPAAISK AFAFPAAISK	36 AKKI LSHTTPEI LSHTTLEI LSHTTPEI AEPL AEPL	0 37 CENPFGYTLQ SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN CKNPLGYALE CKNPLGYALE	0 38 LVKQTKVDVT LLNGSVKQCN LLNGSVKQCN LLNGSVKQCN LVKKAKATHN LVKKAKATHN	0 39 EEYMRSAAD- GDYFETFKGK GDYFETFKGK GDYFETFKGK EEYLRSVAD- EEYLRSVAD-	0 40 EGYGRMCEYL EGYGSMCEYL EGYGRMCEYL L	410 MAMKGRPHFT DFQRTMSSME DFQRTMSSME DFQRTMSSME LVLRGRPQYS LVLRGRPQYS	42 	0 43 VTRAGFGLVD WTNF - FNPLD WTNF - FNPLD WTNF - FNPLD NTRVGFGDVN NTRAGFGDVN	ecne RTSW ECNE - RTSW ECNE - RTSW ECNE - RTSW ECNE - RTSW ECNE - QPVF ECNE - QPVF	0 45 GGPAKGGVGP IGVAGKIESA IGVAGKIESA IGVAGKIESA AGPVKA AGPAKA
VрААТ1 F¢ААТ1 FvААТ FаААТ MpААТ1 MdААТ2 P¢ААТ1	31(IALQP - DPE AASRALTSGT ATSRALTSGT AASRALTSGT LALNI - NPK LALNI - NPK LVLKI - NPK	0 32 EEMRVICVVN TSTRLSIAAQ TSTRLSIAAQ EAVRVSCIVN QAVRVSCIVN QAVRVSCIVN	0 33(SRTKLN- AVNLRTRMNM AVNLRTRMNM ARGKHNN ARGKHNN ARGKHNN	9 34 PPLPTGPYGN ETVLDNATGN ETVLDNAIGN ETVLDNATGN VRLPLGYYGN VRLPLGYYGN VHIPLGYYGN	0 350 GIAFPAAISQ LIWWAQAILE LIWWAQAILE LPWWAQAILE AFAFPAAISK AFAFPAAISK AFAFPAAISK	36 AKXI LSHTTPEI LSHTTPEI LSHTTPEI AEPL AEPL AEPL	0 37 CENPFGYTLQ SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN CKNPLGYALE CKNPLGYALE CKNPLGYALE	0 38 LVKQTKVDVT LLNGSVKQCN LLNGSVKQCN LLNGSVKQCN LVKKAKATMN LVKKAKATMN	10 39 C EEYMRSAAD- C GDYPETFKGK G GDYPETFKGK C EGYPETFKGK E EEYLRSVAD- E EEYLRSVAD- E EEYLRSVAD-	0 40 L EGYGRMCEYL EGYGRMCEYL EGYGRMCEYL 	410 MAMKGRPHFT DFQRTMSSME DFQRTMSSME LVLRGRPQYS LVLRGRPQYS LVLRGRPQYS	42 WVRRY-MVSD PAPDIYLFSS PAPDIYLFSS STGSYLIVSD STGSYLIVSD STGSYLIVSD	0 43 VTRAGFGLVD WINF-FNPLD WINF-FNPLD WINF-FNPLD NIRVGFGDVN NTRAGFGDVN	GNG RTSW GNG RTSW GNG RTSW GNG RTSW GNG RTSW GNG QPVP GNG QPVP GNG QPVP	0 45 GGPAKGGVGP IGVAGKIESA IGVAGKIESA IGVAGKIESA AGPVKA AGPAKA
VPAAT1 FCAAT1 FVAAT MPAAT1 MDAAT1 MdAAT2 PCAAT1 RhAAT	31(IALQP - DPE AASRALTSGT ATSRALTSGT AASRALTSGT LALNI - NPK LALNI - NPK LVLKI - NPK LVLKI - NPK	0 32 EEMRVICVVN TSTRLSIAAQ TSTRLSIATQ TSTRLSIATQ TSTRLSIATQ EAVRVSCIVN GAVRVSCIVN TSTRFSVASQ	SRTKLN- SRTKLN- AVNLRTEMMM VVNIRSRRMM AVNLRTEMMM ARGKHNN ARGKHNN TVNLRSEMMM	9 34 PPLPTGFYGN ETVLDNATGN ETVLDNATGN ETVLDNATGN VRLPLGYYGN VRLPLGYYGN VHIPLGYYGN KTTLDNAIGN	0 350 GIAFPAAISQ LIWWAQAILE LIWFAPAILE LFWFAPAILE AFAFPAAISK AFAFPAAISK AFAFPAAISK IFLWASARLD	36 AKKI LSHTTPEI LSHTTPEI LSHTTPEI AEPL AEPL AEPL AEPL LNDTAPGS	0 37 CENPFGYTLQ SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN CKNPLGYALE CKNPLGYALE CKNPLGYALE SDLKLCDLVN	0 38 LVKQTKVDVT LLNGSVKQCN LLNGSVKQCN LVKAKATMN LVKKAKATMN LVKKAKATMN LVKKAKATMN	10 39 C EEYMRSAAD- 1 GDYPETPKGK 1 GDYPETPKGK 2 GDYPETPKGK 2 EEYLRSVAD- 2 EEYLRSVAD- 3 EEYLRSVAD- 4 EEYLRSVAD- 4 EEYLRSVAD-	0 40 	410 MAMKGRPHFT DFQRTMSSME DFQRTMSSME LVLRGRPQYS LVLRGRPQYS LVLRGRPQYS DFMEEGSFVE	42 VVRRY-MVSD PAPDIYLFSS PAPEIYLFTS STGSYLIVSD STGSYLIVSD STGSYLIVSD PAPEFYSFSS	0 43 VTRAGFGLVD WINF-FNPLD WINF-FNPLD WINF-FNPLD NTRVGFGDVN NTRAGFGDVN WTRF-FDQVD	GNG RTSW GNG RTSW GNG RTSW GNG RTSW GNG RTSW GNG QPVP GNG QPVP GNG QPVP GNG QPVP	0 45 GGPAKGGVGP IGVAGKIESA IGVAGKIESA IGVAGKIESA AGPVKA AGPAKA VGFSGRVETR
УрААТ1 FсААТ1 FvAAT FaAAT MgAAT1 MdAAT2 PcAAT1 RhAAT MgAAT1	31(D 32 EEMRVICVVN TSTRLSIAAQ TSTRLSIATQ TSTRLSIATQ EAVRVSCIVN QAVRVSCIVN TSTRFSVASQ VDVHVCFFAN	SR TKLN- AVNLRTRMNM VVNIRSRNM AVNLRTRMNM AR GKHNN AR GKHNN AR GKHNN TVNLRSKMNM TRHLLRQVVL	PPLPTGFYGN ETVLDNATGN ETVLDNATGN ETVLDNATGN VRLPLGYYGN VRLPLGYYGN VHIPLGYYGN KTTLDNAIGN LPPEDGYYGN	0 350 GIAFPAAISQ LIWWAQAILE LIWFAPAILE LFWWAQAILE AFAFPAAISK AFAFPAAISK AFAFPAAISK IFLWASARLD CFYPVTATAP	36 LSHTTPEI LSHTTPEI LSHTTPEI AEPL AEPL AEPL LHDTAPGS SGRI	0 37 CENFFGYTLQ SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN CKNPLGYALE CKNPLGYALE SDLKLCDLVN ASAELIDVVS	0 38 LVKQTKVDVT LLNGSVKQCN LLNGSVKQCN LVKKAKATMN LVKKAKATMN LVKKAKATMS LINESIKEFN IIRDAKSRLF	C EEYMRSAAD GDYFETFKGK GDYFETFKGK GDYFETFKGK EEYLRSVAD EEYLRSVAD EEYLRSVAD SDYLEILKGK GEFAKWAAG	0 40 	410 MAMKGRPHFT DFQRTMSSME DFQRTMSSME LVLRGRPQYS LVLRGRPQYS LVLRGRPQYS DFMEEGSFVE FKDD-PYELS	42 VVRRY-MVSD PAPDIYLFSS PAPEIYLFSS STGSYLIVSD STGSYLIVSD STGSYLIVSD STGSYLIVSD PAPEFYSFSS FTYNSLFVSD	0 43 VTRAGFGLVD WINF-FNPLD WINF-FNPLD NTRVGFGDVN NTRAGFGDVN NTRAGFGDVN WTRF-FDQVD WTRLGFLDVD	FONG PEPVY CMG RTSW CMG RTSW CMG RTSW CMG QPVP CMG QPVP CMG QPVP CMG QPVP CMG RPSW XGMG KPLH	0 45 GGPAKGGVGP IGVAGKIESA IGVAGKIESA IGVAGKIESA AGPVKA AGPAKA VGFSGRVETR VIPFAYLDIM
УрААТ1 РСААТ1 РУААТ РАААТ МДААТ2 РСААТ1 RhAAT МБААТ1 СтаАТ1	31(EEMRVICVVN TSTRLSIAAQ TSTRLSIAAQ TSTRLSIAAQ EAVRVSCIVN QAVRVSCIVN QAVRVSCIVN TSTRFSVASQ VDVHVCFFAN EEVRFLCVMN	SRTKLN- AVNLRTEMNM VVNIRSRENM AVNLRTEMNM ARGKHNN ARGKHNN ARGKHNN TVNLRSKMNM TRHLLRQVVL LRSKID-	PPLPTGFYGN ETVLDNATGN ETVLDNATGN ETVLDNATGN VRLPLGYYGN VRLPLGYYGN VHIPLGYYGN KTTLDNAIGN LPPEDGYYGN IPLGYYGN	0 350 GIAFPAAISC LIWWAQAILE LIWWAQAILE AFAFPAAISK AFAFPAAISK AFAFPAAISK IFLWASARLD CFYPVTATAP AVVVPAVITT	36 	0 37 CENPFGYTLQ SDLKLCDLVN SDLKLCDLVN CKNPLGYALE CKNPLGYALE CKNPLGYALE SDLKLCDLVN ASAELIDVVS CGNPLGYAVD	0 38 LVKQTKVDVT LLNGSVKQCN LLNGSVKQCN LVKAKATMN LVKKAKATMN LVKKAKATMN INRSINEFN IIRDAKSRLF LIRKAKAT	10 39 EEYMRSAAD- I GDYPETFKGK GDYPETFKGK EEYLRSVAD- EEYLRSVAD- EEYLRSVAD- SDYLEILKGK GEFAKWAAG- MEYIKSTVD-	0 40 EGYGRMCEYL EGYGRMCEYL EGYGRMCEYL L EGYGGMCDLL L	410 MAMKGRPHFT DFQRTMSSME DFQRTMSSME DFQRTMSSME LVLRGRPQYS LVLRGRPQYS LVLRGRPQYS DFMEEGSFVE FKDD-PYELS MVIKGRPYFT	42 VVRRY-MVSD PAPDIYLFSS PAPEIYLFTS PAPEIYLFTS STGSYLIVSD STGSYLIVSD STGSYLIVSD PAPEFYSFSS FTYNSLFVSD VVGSF-MMSD	0 43 VTRAGFGLVD WINF-FNPLD WINF-FNPLD WINF-FNPLD NTRAGFGDVN NTRAGFGDVN NTRAGFGDVN WTRLGPLDVD LTRIGVENVD	44 GMG RPEPVY GMG RTSW GMG RTSW GMG RTSW GMG RTSW GMG RTSW GMG RPVP GMG QPVP GMG RPVW GMG KPLH GMG KAIF	0 45 GGPAKGGVGP IGVAGKIESA IGVAGKIESA IGVAGKIESA AGPVKA AGPAKA AGPAKA VGF5GRVETR VIPFAYLDIM GGFTTTGARI
VDAAT1 FcAAT1 FvAAT FaAAT MdAAT2 FcAAT1 RhAAT MsAAT1 CmAAT2 CmAAT2	31(IALOP DPE AASRALTSGT ATSRALTSGT IALNI NPK LALNI NPK LVLKI NPK LVLKI NPK AASRALSSG- RAINL DPG IALQF KPE IAFQL KPE	22 EEMRVICVVN TSTRLSIAAQ TSTRLSIAAQ TSTRLSIAAQ EAVRVSCIVN QAVRVSCIVN TSTRFSVASQ VDVHVCFFAN EEVRFLCVMN	SRTKLN- AVNLRTRMNM VVNIRSRRMM AVNLRTRMNM ARGKHNN ARGKHNN ARGKHNN TVNLRSKMNM TRHLLRQVVL LRSKID- LRSKID-) 34 PPLFUGYGN ETVLDNATON ETVLDNATON ETVLDNATON VRLPLGYYGN VRLPLGYYGN VRLPLGYYGN KTTLDNAIGN LPPEDGYYGN - IPLGYYGN - IPLGYYGN	0 350 GIAFPAAISQ LIWAQAILE LIWAQAILE LPWWAQAILE AFAFPAAISK AFAFPAAISK AFAFPAAISK IFLWASARLD CFYPVTATAP AVVVPAVITT AVVPPAVITT	36 LSHT-TPEI LSHT-TPEI LSHT-TPEI LSHT-TPEI AEPL LNDT-APGS SGRI AAXL VAXL	0 37 CENPFGYTLQ SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN CKNPLGYALE CKNPLGYALE CKNPLGYALE SDLKLCDLVN ASABLIDVVS CGNPLGYAVD CGNPLGYAVD	0 38 LVKQYKVDY LLNGSVKQCN LVKKAKATNN LVKKAKATNN LVKKAKATNN LINESIKEFN IIRDAKSRLF LIRKAKAT	C 39 C EEYMRSAAD- GDYPETPKGK GDYPETPKGK EDYPETPKGK EEYLRSVAD- EEYLRSVAD- EEYLRSVAD- SDYLEILKGK GEFAKWAAG- MEYIKSTVD- KEYIKSNVD-	0 400	410 MAMKGRPHFT DFQRTMSSME DFQRTMSSME LVLRGRPQYS LVLRGRPQYS LVLRGRPQYS DFMEEGSFVE FKDD-PYELS MVIKGRPYFT MVIKGRPFT	42 VVRRY-WYSD PAPDIYLFSS PAPDIYLFSS STGSYLIVSD STGSYLIVSD STGSYLIVSD PAPEFYSFSS FTINSLFVSD VVGSF-MMSD EIGFF-MMSD	0 43 VTRAGFGLVD WTNF-FNPLD WTNF-FNPLD WTNF-FNPLD NTRAGFGDVN NTRAGFGDVN WTRF-FDQVD WTRLGFLDVD LTRIGVENVD	44 GWG RPEPVY GWG - RTSW GWG - RTSW GWG - RTSW GWG - QPVF GWG - QPVF GWG - QPVF GWG - RFSW GWG - KAIF GWG - KAIF	0 45 GGPAKGGVGP GGPAKGGVGP IGVAGKIESA IGVAGKIESA IGVAGKIESA AGPAKA AGPAKA VGPSGRVETR VIPPAYLDIM GGPTITGARI GGPIIGGCGI
VPAAT1 FcAAT1 FvAAT MpAAT1 MdAAT2 PcAAT1 RhAAT CmAAT1 CmAAT2 CmAAT3	310 IALQP-DPE AASRALTSGT AASRALTSGT LALNI-NPK LALNI-NPK LVLKI-NPK AASRALSSG RAINL-DPG IALQPKPE IARQLKPE ISLQP-DPE	321 SERVEVICUUN TSTRLSIAAQ TSTRLSIAAQ TSTRLSIAAQ TSTRLSIAAQ QAVRVSCIVN QAVRVSCIVN QAVRVSCIVN TSTRFSVASQ VDVHVCPFAN EEVRFLCVMN EEVRFLCVMN	SRTKLN- SRTKLN- AVNLRTRNNM VVNIRSRNM AVNLRTRNM ARGKINN ARGKINN ARGKINN TVNLRSKNM TRHLLRQVVL LRSKID- LRSKID- LRSKID-	PPLPTGFYGN ETVLDNATGN ETVLDNATGN ETVLDNATGN ETVLDNATGN VRLPLGYYGN VRLPLGYYGN VHIPLGYYGN - IPLGYYGN - IPLGYYGN PLPTGYYGN	0 350 GIAFPAAISQ LIWWAQAILE LIWWAQAILE LIWWAQAILE LIWWAQAILE LIWWAQAILE LIWWAQAILS AFAFPAAISK AFAFPAAISK AFAFPAAISK IFLMASARLD CFYPVIATA AVVVPAVITT AIVFPAVITT AFAFPVALTT	36 AKK LSHT TPEI LSHT TPEI LSHT TPEI LSHT TPEI AEP L AEP L LNDT APGS SGR I AAK L VAK L VAK L AGK L	0 37 CENPFGYLQ SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN ASAELIDVVS CGNPLGYAVD CGNPLGYAVD	0 38 LVKQTKVDVT LLNGSVKQCN LLNGSVKQCN LVKKAKATNN LVKKAKATNN LVKKAKATNN LINESIKEFN I IRDAKSRLF LIRKAKAKAT LIRKAKAKAT	10 39 2 EFYMRSAAD- 2 EFYMRSAAD- 3 GDYFETFKGK 3 GDYFETFKGK 4 GEYLRSVAD- 4 EFYLRSVAD- 4 EFYLRSVAD- 5 SDYLEILKGK 5 GFAKNAAG- 2 MEYIKSTVD- 5 KEYIKSVAD- 3 KEYKSVAD- 3 KEYKSVAD- 3 CEDYMKSVAD- 3 CEDYMENT	0 400 EGYGRMCEYL EGYGRMCEYL EGYGRMCEYL EGYGRMCEYL EGYGRMCELL EGYGRMCELL EGYGRMCELL EGYGRMCELL EGYGRMCELL EGYGRMCEYL	410 MAMKGRPHFT DFQRTMSSME DFQRTMSSME DFQRTMSSME DFQRTMSSME LVLRGRPQYS LVLRGRPQYS LVLRGRPQYS DFMEEGSFVE FKDD-FYELS MVIKGRPHFT MVIKGRPHFT	42 WVRRY-MVSD PAPDIYLFSS PAPEIYLFTS PAPEIYLFTS STGSYLIVSD STGSYLIVSD STGSYLIVSD STGSYLIVSD STGSYLIVSD STGSYLIVSD STGSYLIVSD STGSYLIVSD BIGPF-MKSD WVRTY-LVSD	VTRAGFGLVD WTNF-FNPLD WTNF-FNPLD WTNF-FNPLD WTNF-FNPLD NTRAGFGDVN NTRAGFGDVN WTRF-FDQVD LTRIGFENVD ITRIGFENVD VTRAGFEDVD	44 FGWC RPEPVY FGWC - RTSW FGWC - RTSW FGWC - RTSW FGWC - QVV FGWC - QVV FGWC - QVV FGWC - RVLH FGWC - KAIF FGWC - KAIF	0 45 , 1, GGPAKGVGP GUAGKIESA IGVAGKIESA IGVAGKIESA IGVAGKIESA JGPAKA AGPAKA VGPSGRVETR VIPPAYLDIM GGPITGGARI GGPITGGARI GGPIGGCGUA
VPAAT1 FcAAT1 FvAAT MpAAT1 MdAAT2 PcAAT1 MsAAT1 CmAAT1 CmAAT2 CmAAT3	311 IALQP DPE AASRALTSGT AASRALTSGT AASRALTSGT LALNI NPK LULNI NPK LULKI NPK LULKI NPK IALQF KPE IAPQL KPE ISLQP DPG KVA DDG	323 Control Control C	33(AVNLRTEMNM VVNLRTEMNM AVNLRTEMNM ARGKHNN ARGKHNN ARGKHNN TVNLRSKMNM TVNLRSKMNM TRHLRQVVL LRSKID- LRSKID- SRSKID- SRSKID-	341 PPLPTGFYGN ETVLDNATGN ETVLDNATGN ETVLDNATGN VRLPLGYYGN VRLPLGYYGN VRLPLGYYGN VRLPLGYYGN - IPLGFYGN - IPLGFYGN PPLLGFYGN PSLGEVGLGN	0 350 GIAFPAATSQ LIWWAQAILE LIWWAQAILE LFWWAQAILE AFAFPAATSK AFAFPAATSK AFAFPAATSK IFLWASARLD CFYPVTATAP AVVVPAVITT AFAFPVALTT AFAFPVALTT INWGTVARHF	36 I AKK	0 37 CENPFGYTLQ SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN CKNPLGYALE CKNPLGYALE SDLKLCDLVN ASAELIDVVS CGNPLGYAVD CGNPLGYAVD CQNPLGYALE SGLELSKLVS	0 38 LVKQTKVDVI LLNGSVKQCN LLNGSVKQCN LVKKAKATMN LVKKAKATMN LVKKAKATMN LINESIKEPN IIRDAKSRLF LIRKAKAKAT LIRKAKAKAT LIRKAKAKAT	10 39 	0 400 EGYGRMCEYL EGYGRMCEYL EGYGRMCEYL EGYGRMCEYL L EGYGMCDLL D D D D D D	410 MAKKGRPHFT MDFQRTMSSME DFQRTMSSME DFQRTMSSME LVLRGRPQYS LVLRGRPQYS DFMEEGSFVE FKD-PYELS MVIKGRPFT MVIKGRPFT MVIKGRPFT MVIKGRPHFT MVIKGRPHFT	42 WVRRY-MVSD PAPDIYLFSS PAPDIYLFSS STGSYLIVSD STGSYLIVSD STGSYLIVSD STGSYLIVSD PAPEFYSFSS FTINSLFVSD EIGPP-MMSD EIGPP-MMSD VVRTY-LVSD VINTY-LVSD	VTRAGFQLVD WTNF-FNPLD WTNF-FNPLD WTNF-FNPLD WTNF-FNPLD WTNF-FNPLD WTRF-FDQVD WTRF-FDQVD WTRF-FDQVD WTRF-FDQVD WTRF-FDQVD VTRAGFBUVD VTRAGFBUVD VTRAGFBUVD	44 	0 45
VPAAT1 FCAAT1 FVAAT FAAAT MPAAT1 MdAAT2 PCAAT1 RhAAT MSAAT1 CMAAT2 CMAAT3 CMAAT3 CMAAT4 CbBBBT	31(IALQP-SPE AASRALTSGT ATSRALTSGT IASRALTSGT IALNI-NPK LALNI-NPK LALNI-NPK IALQF-RE IALQF-RE ISLQP-SPE VADPE KVANPD	32: EEEMEVICOVN TSTRLSIAAQ TSTRLSIAAQ TSTRLSIAAQ EAVEVSCIVN TSTRFSVASQ QAVEVSCIVN TSTRFSVASQ QAVEVSCIVN TSTRFSVASQ EEVEFLCVNN EEVEFLCVNN EEVEFLCVNN DSQRFSTLSH EEVENICIVN	330 SRTKLN- AVNLRTRNMM AVNLRTRNMM AVNLRTRNMM ARGKINN ARGKINN TVNLRSKNM TVNLRSKNM TVNLRSKNM LRSKID- SRSKIP- SRSKFN- VVNLR-KKLE ARSKFN-	341 PPLPTGFYGN ETVLDNATGN ETVLDNATGN ETVLDNATGN ETVLDNATGN VRLPLGYYGN VRLPLGYYGN VRLPLGYYGN - IPLGYYGN PPLPDGYYGN PSLGEVSLGY	0 350 GIAPPAAISQ LIWMAQAILE LIWMAQAILE LIWMAQAILE LIWMAQAILE LIWMAQAILE LIWMAQAILE AFAPPAAISK AFAPPAAISK AFAPPAAISK AFAPPAAISK AFAPPAAVITT IMMOTVAHIP IMMOTVAHIP	36 LSHTTPEI LSHTTPEI LSHTTPEI LSHTTPEI LSHTTPEI LSHTTPEI LSHTTPEI LSHTTPEI LSHTTPEI SGR	0 37 CENPFQYLQ SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN ASAELIDVVS CGNPLGYAVD CQNPLGYALE EGLELSKLVS CNNPLGYALE	0 38 LVKQTKVDVI LLNGSVKQCN LLNGSVKQCN LVKKAKATNN LVKKAKATNN LVKKAKATNN LVKKAKATNN LINESIKEFN IIRDAKSRLF LIRKAKAKAT LVRKAKADVI LLRQSFKKIN LIRKAKREVT	10 39 	0 400 L BGYGRMCEYL EGYGRMCEYL EGYGRMCEYL EGYGRMCEYL EGYGRMCEYL EGYGRMCEYL EGYGRMCEYL GDKERRNOVE	410 MAKKGRPHPT DPQRTMSSME DPQRTMSSME UVLRGRPQYS LVLRGRPQYS LVLRGRPQYS LVLRGRPQYS MVIKGRPYPT MVIKGRPHPT KLVQEIN-KW MVATGRPHPT	42 WVRRY-MVSD PAPDIYLFSS PAPDIYLFSS STGSYLIVSD STGSYLIVSD STGSYLIVSD STGSYLIVSD STGSYLIVSD STGSYLIVSD STGSYLIVSD STGSYLIVSD WVRSY-MVSD VVRTY-LVSD PISNYYFFTS VVNTY-LVSD	0 433 VTRAGFQLVD WTNF-FNPLD WTNF-FNPLD NTRVGFQDVN NTRAGFQDVN WTRAGFQDVN WTRLGFLDVD LTRIGFENVD VTRAGFQDVD VTRAGFQDVD WKNLKLNEVD VTRAGFQDVD	44 GWG PEPYY GWG RTSW GWG RTSW GWG RTSW GWG QPVP GWG QPVP GWG QPVP GWG QPVP GWG RPSW YGWG KAIF GWG KAIF GWG KAIF GWG KAIF GWG RANY GWG RANY	0 45 GGPAKGGVGP IGVAGKIESA IGVAGKIESA IGVAGKIESA IGVAGKIESA AGPYKA AGPAKA AGPAKA AGPAKA AGPAKA GGPITGARI GGPITGARI GGPAKGGVGX SAIAGDPNEM
VPAATI FCAATI FVAAT MPAATI MAATI RhAAT MBAATI CMAATI CMAATI CMAATI CMAATA CDBEAT	311 IALQP-DPE AASRAITSGT ATSRAITSGT IALNI-NPK LALNI-NPK LALNI-NPK LALNI-NPK LALNI-NPK IALGP-FKPE IALQP-FKPE ISLQP-DPE ISLQP-DPE ENCAK-KEO	32: 	33(AVNLRTRANM AVNLRTRANM AVNLRTRANM AVNLRTRANM ARGKINN ARGKINN TVNLRSKNMM TRHLLRQVUL LRSKID- LRSKID- LRSKID- LRSKID- CRSKID- CRSKID- CRSKID- VVNIR-KMLE ARSKID-	944 PPLPTGFYGN ETVIDNATGN ETVIDNATGN ETVIDNATGN VRLPLGYYGN VRLPLGYYGN VRLPLGYYGN VRLPLGYYGN PPLGFYGY PPLDFGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDFUYGY	0 350 GIAFPAAISQ LIWWAQAILE LIWWAQAILE LIWWAQAILE LFWMAQAILE LFWMAQAILE AFAFPAAISK AFAFPAAISK JFAFPAAISK IFLMASARLD CPYPVTATAP AVVVFAVITT AIVPFAVITT IMMGTVAHHF AFAIPAAVTT IMMGTVAHHF AFAIPAAVT	36 LSHTTPEI LSHTTPEI LSHTTPEI LSHTTPEI AEPL AEPL LNDTAFGS SGRI AAKL AAKL STRNEEF AGKL STTRNEEF AGKL ITVAFKITL	0 37 	0 38 LVXQTKVDVI LLNGSVKQCN LLNGSVKQCN LVKKAKATNN LVKKAKATNN LINESIKEFN I IRDAKSRLF LIRKARATN LIRKARATN LIRKARATN LIRKARATN LIRKARATN LIRKARATN LIRKARATN	10 39 C.EXYMRSAD- 1 GDYPETPKGK 1 GDYPETPKGK 1 GDYPETPKGK 1 EEYLRSVAD- 2 EEYLRSVAD- 2 EEYLRSVAD- 3 SDYLEILKGK 9 GEPAKWAAG- 1 SDYLEILKGK 2 EEYMKSVAD- 4 KDYIKELING 2 EEYMKSVAD- 4 KDYIKELING 2 EEYMKSVAD- 4 KDYIKELING	0 400L EGYGRMCEYL EGYGRMCEYL EGYGRMCEYL EGYGRMCEYL EGYGRMCELL EGYGRMCELLL EGYGGMCDLLL GDKERRNGVM	410 MAKKGPHFT DFQRTMSSME DFQRTMSSME LVLRGRPQYS LVLRGRPQYS LVLRGRPQYS DFMEGGFVE FKDD-PYELG WVIKGRPFTT MVIKGRPFTT KLVGEIN-KW MVATGRPHFT	42 WVRRY-MVSD PAPDIYLFSS PAPDIYLFSS STGSYLIVSD STGSYLIVSD STGSYLIVSD PAPDFYSFSS VVNSP-MMSD EIGPF-MMSD EIGPF-MMSD PISNYYFFIS VVNTY-LVSD PISNYYFFIS VVNTY-LVSD	0 433 VTRAGFGLVD WTNP-FNPLD WTNP-FNPLD WTNP-FNPLD NTRAGFGDVN NTRAGFGDVN WTRLGFLVD UTRLGFLVD UTRLGFLVD VTRAGFGEVD VTRAGFGEVD VTRAGFGEVD VTRAGFGEVD VTRAGFGEVD VTRAGFGEVD	44 FGN0 RPEPVY FGW0 - ETSW FGW0 - ETSW FGW0 - CPVF FGW0 - OPVF FGW0 - OPVF FGW0 - OPVF FGW0 - CPVF FGW0 - KAIF FGW0 - KAIF FGW0 - KAIF FGW0 - KAIF FGW0 - KAIF FGW0 - EXVY FGW0 - EXVY F	0 45 GGPAKGGVGP IGVAGKIESA IGVAGKIESA IGVAGKIESA AGPYKA
VPAATI FCAATI FVAAT PAAAT MPAATI MAAAT2 PCAATI MBAAT1 CMAAT2 CMAAT3 CMAAT3 CMAAT4 CbBEBT	111 IALQP - DPE AASRALTSGT ATSRALTSGT IALNI - NPK LALNI - NPK LALNI - NPK LALNI - NPK IALQL - KPE IAFQL - KPE ISLQP - SPE KVA DPE KVA NPD EMCAK - KEQ	32: EEMRVICCVN TSTRLSIARQ TSTRLSIARQ TSTRLSIARQ TSTRLSIARQ EAVRVSCIVN QAVRVSCIVN QAVRVSCIVN TSTRFSVARQ QUVHVCFPAN EEVRFLCVNN EEVRFLCVNN DSQRPSTLSH EEVRICIVN TKSRPSLMVH	330 SRTKLN- AVNLRTRINN AVNLRTRINN AVNLRTRINN ARGKINN ARGKINN TRHLLRQVVL LRSKID- SRSKID- SRSKID- SRSKIN- VVNIR-KML ARSKIN-	341 PPLPTGFYGN ETVLDNATGN ETVLDNATGN ETVLDNATGN VRLPLGYYGN VRLPLGYYGN VHIPLGYYGN - IPLGFYGN PSLGEVSLGN LALENDVSGN	0 350 GIAPPAAISQ LIWWAQAILE LIWWAQAILE LIWWAQAILE LFWWAQAILE LFWWAQAILE LFWWAQAILE LFWWAQAILE LFWWAQAILE LFWWAQAILE CFYPVIATA AVVVPAVITT JFWWAYAUTT IMWGTVAHHF FFIVVNAESK	36 LSHT-TPEI LSHT-TTEI LSHT-TTEI LSHT-TTEI LSHT-TTEI AEPL AEPL AEPL SGRI AAKL SGRL STTR-NEEF AGKL ITVAPKITDL	0 37 	0 38 LVXQTKVDVT LLNGSVKQCN LLNGSVKQCN LVKKARATNN LVKKARATNN LVKKARATNN LINESIKEPN LIRKARATI LIRKARATI LIRKARATI LIRKARATI LIRKARATI LIRKARATI LIRKARATI LIRKARATI LIRKARATI LIRKARATI	10 39 	0 400 BGYGRMCEYL EGYGRMCEYL EGYGRMCEYL L EGYGRMCEYL L EGYGRMCEYL L EGYGRMCEYL C C C C C C C C C C C C C	410 MAKKGPHFT DFQRTMSSME DFQRTMSSME LVLRGRPQYS LVLRGRPQYS DFMEEGSFVE FKDD-FYELS MVIKGRPFT MVIKGRPHFT KLVGEIN-KW MVATGRPHFT VREFYYEWGK	42 VVRRY-MYSD PAPDIYLFSS STGSYLIVSD STGSYLIVSD STGSYLIVSD STGSYLIVSD PAPEFYSFSS STGSYLIVSD PAPEFYSFSS STGSF-MKSD VVRTY-LVSD PISNYFFTS GEKNVFLYTS	VTRAGFGUVD WTNF-FNPLD WTNF-FNPLD WTNF-FNPLD NTRUGFGUVN NTRAGFGUVN WTRF-FDQUD LTRIGVENVD UTRLGPENVD VTRAGFEUVD WKNLKLNEVD WTRLGFELYEVD	44 FGNG PEPVY FGNG - RTSW FGNG - RTSW FGNG - RTSW FGNG - QPVP FGNG - QPVP FGNG - QPVP FGNG - CPVP FGNG - KPLH FGNG - KAIP FGNG - KAIP FGNG - KAIP FGNG - KAIP FGNG - EAVY FGNG - EAVY	0 45 GGPAKGGVGP IGVAGKIESA IGVAGKIESA AGPYKA XGPAKA XGPSGRVETE VIPPAYLDIM GGPTIGGCGI GGPAKGGVGA SAIAGDPNEM GGPAKGGVGA SAIAGDPNEM
VDAAT1 FCAAT1 FVAAT FAAAT MDAAT1 MAAAT2 FCAAT1 MBAAT1 CMAAT3 CMAAT3 CMAAT4 CbBEAT CbBEAT	1111 IALQPDE AASSALTSGT AASSALTSGT AASSALTSGT IALXINFK LALXINFK LALXINFK LVLKINFK AASSALSGO- IALQPKFE IAVQLKFE IAVQLKFE IAVQ-	32: EEMKVICUVN TSTRLSIATQ TSTRLSIATQ TSTRLSIATQ TSTRLSIATQ TSTRFSVASQ VDVNVCFPAN EEVKFLCVMN EEVKFLCVMN EEVKFLCVMN EEVKFLCVNN EEVKFLCVNN EEVKFLCVNN EEVKFLCVNN ASQRFSTLSH EEVKNICTVN ASQRFSTLSH EEVKNICTVN ASQRFSTLSH EEVKFLCVNN ASQRFSTLSH EEVKFLCVNN ASQRFSTLSH EEVKFLCVNN ASQRFSTLSH EEVKFLCVNN ASQRFSTLSH EEVKFLCVNN ASQRFSTLSH EEVKFLCVNN ASQRFSTLSH EEVKFLCVNN ASQRFSTLSH EEVKFLCVNN ASQRFSTLSH EEVKFLCVNN ASQRFSTLSH EEVKFLCVNN ASQRFSTLSH EEVKFLCVNN ASQRFSTLSH EEVKFLCVNN EEVKFLCVNN EEVKFLCVNN EEVKFLCVNN EEVKFLCVNN EEVKFLCVNN EEVKFLCVNN EEVKFLCVNN EEVKFLCVNN EEVKFLCVNN EEVKFLCVNN ASQRFSTLSH EEVKFLCVNN E	333 SRTKLN- AVNLRTENNM AVNLRTENNM ARGKINN ARGKINN ARGKINN ARGKINN LRSKID- LRSKID- LRSKID- SRSKID- SRSKID- SRSKID- SRSKID- SRSKID- SRSKID- SRSKID- SRSKID- A	34 PPLPTGYYGN ETVLDNATGN ETVLDNATGN ETVLDNATGN ETVLDNATGN VRLPLGYYGN VRLPLGYYGN VHIPLGYYGN - IPLGYYGN - IPLGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLDGYYGN PPLGATGYYGN PPLGATGYYGN PPLGATGYYGN PPLGATGYYGN PPLGATGYYGN AG	GIAPPAAISQ GIAPPAAISQ LIWWAQAILE LIWWAQAILE LIWWAQAILE LIWWAQAILE LIWWAQAILE LIWWAQAILE APAPPAAISK APAPPAAISK APAPPAAISK APAPPAAISK APAPPAVITT AIVPPAVITT AIVPPAVITT AFAPPVALTT PFIVVNAESK	36 AKX I LSHT -TPEI LSHT -TPEI LSHT -TPEI AEP L AEP L LSHT -TPEI LSHT -TLEI LSHT -TLEI XAEP L XAEP L XAE L XAK L XAK L XAK L STTR - NEEF AGK L 51	0 37 CENPFGYIQ SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN CKNPLGYALE CKNPLGYALE CKNPLGYALE CCNPLGYALE CCNPLGYAVD CCNPLGYAVD CCNPLGYALE SGLELSKLVS CNNPLGFALE TESLGSACGE	0 38 LVKQTKVDVI LLNGSVKQCN LLNGSVKQCN LVKKAKATMS LVKKAKATMS LVKKAKATMS LINESIKEPN IIRDAKSRLP LIRKAKAKAT LIRKAKAKAT LIRKAKAKAT LIRKAKAKAT LIRKAKAKAT LIRKAKAKAT IISEVAKVDD	10 39 CEYMSSAD- GDYPETFKGK GDYPETFKGK GDYPETFKGK GDYPETFKGK GDYPETFKGK SULSSAD- EEYLRSVAD- EEYLRSVAD- CEFAKNAAG CEFA	0 400	410 MANKGRPHFT DFQRTMSSME DFQRTMSSME LVLRGRPQYS LVLRGRPQYS LVLRGRPQYS KLVGRPFT MVIKGRPHFT MVIKGRPHFT VREPYYEWGK	42 WVRRY-MVSD PAPDIYLFSS PAPDIYLFSS STGSYLIVSD STGSYLIVSD STGSYLIVSD PAPEFYSFSS VVGSP-MMSD EIGPF-MMSD EIGPF-MMSD PISNYYFFTS VVNTY-LVSD GEKNVFLYTS	0 433 VTRAGFQLVD WTNF-FNCLD WTNF-FNCLD WTNF-FNCLD NTRAGFQDVN NTRAGFQDVN WTRF-FDCVD WTRF-FDCVD UTRIGFBVVD UTRIGFBVVD VTRAGFQEVD WKNLKLNEVD VTRAGFQEVD	44 FGN0RPEPVY FGN0 - RTSW FGN0 - RTSW FGN0 - RTSW FGN0 - QPVP FGN0 - QPVP FGN0 - QPVP FGN0 - QPVF FGN0 - QPVF FGN0 - RSLH FGN0 - KAIY FGN0 - KAIY FGN0 - KAIY FGN0 - KAIY FGN0 - EXLW FGN0 - EXLW	0 45 GGPAKGGVGP IGVAGKIESA IGVAGKIESA IGVAGKIESA IGVAGKIESA IGVAGKIESA IGVAGKIESA VGPSGKVETR VIPPAYLDIT GGPIIGGCGI GGPAKGGVGA SAIAGDPHEM GGPAKGGVGA IPSLVDTTAV
VPAATI FCAATI FVAAT FBAAT MGAAT2 FCAATI MBAATI CMAAT2 CMAAT3 CMAAT4 CbBEBT CbBEAT	1ALQPDPE AASRALTSGT ATSRALTSGT AASRALTSGT LALNI-NPK LALNINPK LALNINPK LVLKINPG IALQFKPE IALQFKPE ISLQPDPE KVADDG EMCCAR-KEQ (464)	32: EEEREVICCVN TSTRLSIARQ EAVRVSCIVN GAVRVSCIVN QAVRVSCIVN QAVRVSCIVN EEVRFLCVN EEVRFLCVN EEVRFLCVN EEVRFLCVVN TKSRPSLNVH CO 47,	330 SRTKIN- AVNLRTENNM AVNLRTENNM AVNLRTENNM ARGKINN ARGKINN ARGKINN TRHLLRQVVL LRSKID- SRSKID- SRSKID- SRSKID- SRSKID- SRSKID- SRSKID- SRSKID- SRSKID- AR-	34 PPLPTGFYGN ETVLDNATGN ETVLDNATGN VRLPLGYYGN VRLPLGYYGN VRLPLGYYGN VHIPLGYYGN VHIPLGYYGN - IPLGFYGN PPLPTGYYGN PPLPTGYYGN LALENDVSGN 9 49	355 GIAPPAAISQ LIWWAQAILE LIWWAQAILE LIWWAQAILE LFWWAQAILE LFWWAQAILE LFWWAQAILE LFWWAQAILE LFWWAQAILE JFAFPAAISK AFAFPAAVSK JFAFPAVALTT INWOTVAHIF FFIVVNAESK 0 500	36 AKX	0 37 CENPFGYIQ SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN CKNPLGYALE CKNPLGYALE CKNPLGYALE CGNPLGYAVD CGNPLGYAVD CQNPLGYALE EGLELSKLVS CNNPLGFALE TESLGSACGE 0 	0 38 LVKQTKVDVI LLNGSVKQCN LLNGSVKQCN LVKKARATN LVKKARATN LVKKARATN LINESIKEFF I FDAKSRLF L TRKARAKT LTRKARKT LIRESIKEFN LIRESIKEFN LIRESIKETN LIRESIKEV I ISEVAKVDI	10 39 CENTRESAD COVPETFICA COVPETFICA COVPETFICA COVPETFICA EXILASIAD EXILASIAD COVPETFICA COVPETFI	0 400 EGYGRMCEYL	410 MANKGRPHFT DFQRTMSSME DFQRTMSSME LVLRGRPQYS LVLRGRPQYS LVLRGRPQYS FKDD-PYELS MVIKGRPHFT MVIKGRPHFT MVIKGRPHFT VRGPHFT VRGPHFT	42 VVRRY-MYSD PAPDIYLFSS STGSYLLFS STGSYLLVSD STGSYLIVSD STGSYLIVSD STGSYLIVSD STGSYLIVSD VVGSP-MKSD VVRY-LVSD GEKNVFLYTS GEKNVFLYTS	0 433 VTRAGFGLVD WTNF-FNELD WTNF-FNELD WTNF-FNELD NTRAGFGDVN NTRAGFGDVN WTRLGFLDVD UTRLGFLDVD UTRLGFLDVD VTRAGFGDVD WKNLKLNSVD VTRAGFGEVD WCREFFLYEVD	44 FGN0 RPBVY FGN0 - RTSW FGN0 - RTSW FGN0 - RTSW FGN0 - RTSW FGN0 - QPVP FGN0 - QPVP FGN0 - QPVP FGN0 - QPVP FGN0 - RSIW YGN0 - KAIF FGN0 - KAIM FGN0 - KAIM	0 45 GGPAKCGYOP IGVACKIESA
VDAATI FCAATI FVAAT FAAAT MDAATI MDAATI MAAAT CMAATI CMAATI CMAATI CDBEAT	311 IALOPDE AASSALTSGT AASSALTSGT LALNI-NFK LALNI-NFK LALNI-NFK LALNI-NFK LALNI-NFK LALNI-FFF ISLOPDEG LALOF-KFE ISLOPDEG LALKP-NFD EMCAK-KEQ 1900TFFFUD	32: EEMRVICUVN TSTRLSIATQ TSTRLSIATQ TSTRLSIATQ TSTRLSIATQ TSTRLSIATQ EAVRVSCIVN QAVRVSCIVN QAVRVSCIVN EXVRJLCVNN EEVRFLCVNN EEVRFLCVNN EEVRFLCVNN SQRPSTLSH EEVRNICIVN MSQRPSTLSH EEVRNICIVN FKNEKGERGI	333 SRTKLN- AVNLRTENNM AVNLRTENNM ARGKINN ARGKINN ARGKINN ARGKINN LRSKID- LRSKID- LRSKID- LRSKID- LRSKID- LRSKID- LRSKID- LRSKID- UNIR-KNLE ARSKIN- VVNIR-KNLE ARSKIN- VVNIR-KNLE ARSKIN- VVNIR-KNLE ARSKIN- VVNIR-SKIP) 34 PPLPTGFYGN ETVLDNATGN ETVLDNATGN ETVLDNATGN ETVLDNATGN VRLPLGYYGN VRLPLGYYGN VRLPLGYYGN -IPLGFYGN -IPLGFYGN PPLPTGFYGN PPLPTGFYGN 9 SLGEVSLGN 49 	GIAPPAAISQ GIAPPAAISQ LIWWAQAILE LIWWAQAILE LIWWAQAILE LIWWAQAILE LPWAQAILE LPWAQAISK APAPPAAISK AP	36 36 37 38 38 38 38 38 38 38 38 38 38	0 37 CENPFGYILQ SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN SDLKLCDLVN ASABLIDVVS CGNPLGYALE CGNPLGYAVE CGNPLGYAVE CGNPLGYAVE CGNPLGYAVE CONFLGYAVE CONFLGYAVE CONFLGYAVE CONFLGYAVE SDLKLCDLVN ASABLIDVVS CONFLGYAVE CONFLGYAVE CONFLGYAVE CONFLGYAVE SDLKLCDLVN SDLK SDLVN SDLK SDLVN SDLK SDLVN SDLK SDLVN SDLK SDLVN SDLK SDLVN	0 38 LVKQTKVDVT LLNGSVKQCN LLNGSVKQCN LVKKAKATMS LVKKAKATMS LVKKAKATMS LINESIKEM IIRDAKSRLF LIRKAKAKT LIRKAKAKT LIRKAKAKT LIRKAKKT LIRKAKKT LIRKAKKT LIRKAKKVT	10 39 CEYMSSAD- 10 GDYPETFKOR 10 GDYPETFKOR 10 GDYPETFKOR 10 EEYLRSVAD- 10 EEYLRSVAD- 10 EEYLRSVAD- 10 EEYLRSVAD- 10 EEYLRSVAD- 10 KEYLKSWAD- 10 KEYLKSWAD- 10 KEYLKSWAD- 10 KEYLKSWAD- 10 KEYLKSWAD- 10 KEYLKSWAD- 10 KEYLKSWAD- 10 KEYLKSWALMO	0 400 L BGYGRMCEYL BGYGRMCEYL BGYGRMCEYL EGYGRMCELL EGYGRMCELL L GGXERRNGVM S	410 MANKGRPHFT DPQRTMSSME DPQRTMSSME DPQRTMSSME UVLRGRPQYS LVLRGRPQYS LVLRGRPQYS LVLRGRPYT MVIKGRPFT MVIKGRPHFT KLVGEIN-KW MVATGRPHFT VREPYYEWGK	42 VVRRY-MYSD PAPDIYLPSS STGSYLIVSD ST	0 433 VTRAGPGLVD WTNP-FNCLD WTNP-FNCLD WTNP-FNCLD WTNP-FNCLD WTRUGFGDVN NTRAGFGDVN WTRP-FOCD WTRAGFGDVD UTRIGFENVD VTRAGFGEVD WKNLKLNEVD VTRAGFGEVD WKNLKLNEVD	44 FGMC P2EVY FGMC - RTSW FGMC - RTSW FGMC - QVVP FGMC - QVVP FGMC - QVVP FGMC - QVVP FGMC - QVVP FGMC - RTSW FGMC - RSW FGMC - KAIF FGMC - KAIF FGMC - KAIF FGMC - KANY FGMC - EXVY FGMC - EXVY	0 45 GGPAKGGVGP IGVAGKIESA IGVAGKIESA IGVAGKIESA IGVAGKIESA IGVAGKIESA IGVAGKIESA IGVAGKIESA VIPBAYLDIT GGPIIGGCGI GGPAKGGVGA GGPAKGGVGA IPSLVDTTAV
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B)



Figure 1. (**A**) Alignment of the deduced VpAAT1 sequence with other acyltransferases of known function from different floral and fruit species. 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 that are characteristic of most AATs are underlined: LVHYYPLAGR, HTMSD (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. At the end of alignment, the percentage of identity with *VpAAT1* is shown. (**B**) Phylogenic analysis of VpAAT1. The phylogenic tree was built using MEGA software (version 4). Numbers on branches indicate bootstrap values (as a percentage). Sequences are the same used in **A** (see above).



Figure 2. DNA gel-blot analysis of genomic DNA from mountain papaya. Genomic DNA (20 μ g per lane) was digested with the indicated restriction enzyme and hybridized with the corresponding ³²P-labeled probe for *VpAAT1*. Hybridization and stringency conditions were as described under Materials and Methods.

of *Bam*HI polymorphism. The *Bam*HI restriction site could be located either in an intron of the VpAAT1 gene or outside the gene. In both cases, this result demonstrates the heterogozity of the plant species and the presence of two different alleles of VpAAT1 gene in the mountain papaya genome. With the aim to localize other AAT genes in mountain papaya, further experiments should be performed with a probe containing an AAT conserved region.

Transcriptional Analysis of VpAAT1. Mountain papaya fruit displayed the typical climacteric rise in ethylene production during ripening at 20 °C (Figure 3A). Treatment of the fruit with 1-MCP inhibited the ethylene production rise by the fruit during ripening, whereas ethylene treatment produces the advancement in time of the climacteric phase development. To estimate the level of VpAAT1 transcript accumulation during ripening of mountain papaya fruit, qPCR analyses were performed (Figure 3B). In control fruit a notorious increment in the level of VpAAT1 transcripts was observed during ripening, reaching the highest level at day 5 and decreasing after that. In 1-MCP-treated fruit VpAAT1 transcripts remained almost constant after treatment, with levels similar to that of day 1. In samples treated with ethylene a clear increment in transcript accumulation was shown during the first days of storage, reaching the maximum level at day 3 and decreasing until the end of the storage period.

Accumulation of VpAATI transcripts was analyzed in several vegetative tissues and fruits at different developmental stages. VpAATI transcripts were detected only in fruit tissues, not being expressed in other vegetative tissues (Figure 3C). A very low transcript level was observed at the large green fruit stage compared to ripe fruit.

AAT Activity during Ripening of Mountain Papaya Fruit. AAT activity showed an increment during ripening of mountain papaya fruit (Figure 4), reaching the maximum level after 3–5 days of storage, followed by a small decline in AAT activity during the remaining days. AAT activity was assayed by its capacity to produce hexyl acetate, one of the main esters



Figure 3. (A) Changes in ethylene production during ripening of mountain papaya fruit. Fruits harvested at the breaker stage were divided into three lots: one was kept untreated (control); another was treated with 1-MCP $(0.3 \,\mu\text{L}\,\text{L}^{-1}$ for 16 h at 20 °C) on the same day of harvest; and the last one was treated with 2 g L⁻¹ Ethrel. After the treatments, the fruit was allowed to ripen at 20 °C. Three replicates of four fruits chosen at random were analyzed every 2 days. The data correspond to the mean \pm SE. (B) Changes in VpAAT1 mRNA abundance during ripening of mountain papaya fruit measured by gPCR. Samples were collected after 1, 3, 5, 7, 9, and 13 days of storage at 20 °C. The expression data correspond to means of three replicates, normalized against $VpEF1-\alpha$ abundance, using a control sample from day 1 as calibrator, and expressed in arbitrary units \pm SE. Asterisks indicate significant differences between control and treatments at the same storage day ($P \le 0.05$). (C) VpAAT1 mRNA abundance in vegetative tissues and fruit samples at different developmental stages. Expression analysis of VpAAT1 by gPCR was performed in flower, small-size green fruit (SGF), medium-size green fruit (MGF), largesize green fruit (LGF), ripe fruit (RF, corresponding to control fruit on day 5), leaf, root, and stem. The expression data are means of three replicates, normalized to $VpEF1-\alpha$ abundance, using a control fruit sample from day 1 as calibrator, and expressed in arbitrary units \pm SE. Asterisks indicate significant differences between tissues ($P \le 0.05$).

produced by mountain papaya fruit. The same profile of AAT activity was observed when activity was assayed by its capacity to produce benzyl acetate (data not shown), an ester that is absent in

mountain papaya's aroma, although maximum activity recorded $(3.2 \text{ pkat mg}^{-1} \text{ of protein})$ was lower than for hexyl acetate.

Functionality of the VpAAT1 Gene. With the aim to evaluate if VpAAT1 protein is functional, the full-length cDNA sequence was cloned and expressed in yeasts. Several transformants were analyzed, and the correct orientation of the insert was checked by means of PCR. The recombinant protein expressed in yeast cells (61.2 pkat mg^{-1} of protein) was partially purified (450 times) through an affinity column (BD Talon), obtaining an enzyme with high specific AAT activity (27548.1 pkat mg^{-1}) toward the formation of benzyl acetate. It is important to note that the ability to synthesize esters was notably diminished in cultures with $OD_{600} > 1$. The activity of the purified enzyme was also assayed in the presence of different combinations of acyl-CoAs and alcohols as substrates (Table 1). The results obtained indicate that the recombinant protein is able to synthesize a wide range of esters when the substrates are provided, including some characteristic aroma compounds from mountain papaya fruit. A marked preference was observed toward the formation of particular compounds: VpAAT1 displayed a strong activity toward



Figure 4. Change in AAT activity during ripening of mountain papaya fruit. Papaya fruit harvested at the breaker stage was allowed to ripen at 20 °C. Fruit extracts were prepared, and AAT activity was quantified by its ability to convert acetyl-CoA and hexanol into hexyl acetate. Data correspond to the mean \pm SE of three replicates.

the formation of benzyl acetate, followed by the ability to synthesize methyl hexanoate, geranyl acetate, and cinnamyl acetate. VpAAT1 showed a moderate activity toward the synthesis of phenylethyl acetate, ethyl hexanoate, and butyl butanoate, and a small activity toward the synthesis of ethyl butanoate, octyl acetate, butyl hexanoate, and hexyl acetate. No activity was registered for the formation of hexyl hexanoate (**Table 1**).

DISCUSSION

Mountain papaya is a climacteric fruit that develops an interesting and characteristic aroma during ripening, which is mainly due to esters (4). Most of the esters identified in mountain papaya fruit are modulated by ethylene, showing an increase in production during ripening and in response to ethylene treatment, and a strong reduction in response to 1-MCP treatment. Because esters are important for aroma, and a significant increase in ester production was observed during ripening of papaya fruit, our study was focused on ester biosynthesis by the AAT enzyme. AAT activity assayed by its capacity to produce hexyl acetate showed an important increment during ripening of mountain papaya fruit, with the maximum level of activity after 5 days of storage at 20 °C.

In addition, an AAT gene sequence was isolated from mountain papaya fruit (VpAAT1) that displays all of the conserved regions observed in other acyltransferases belonging to the BAHD superfamily. A large number of acyltransferases have been described in plants, with 61 and 91 putative members in Arabidopsis and Populus, respectively. In some fruit species, such as melon and apple, a small multigene family has been described (12-14). To determine the complexity of AAT genes present in mountain papaya's genome, DNA gel-blot analysis was performed. Our results suggest the existence of two different alleles of the VpAAT1 gene in mountain papaya. Phylogenic analysis indicated that VpAAT1 is close to other AAT genes belonging to subfamily III that participate in the synthesis of volatile compounds during fruit ripening, such as CmAAT1, CmAAT3, PcAAT1, MpAAT1, and MdAAT2 (12). In addition, members of subfamily III have been described for their capacity to produce benzyl acetate (28). Interestingly, benzyl acetate has not been described in mountain papaya fruit aroma (4, 30, 31). According to our phylogenic analysis, the most similar sequences to VpAAT1 are CmAAT3 and CbBEBT, and all of them displayed the highest activity toward the synthesis of benzyl acetate (Table 2). CbBEBT and VpAAT1 displayed similar activity toward the synthesis of cinnamyl acetate (8.4 and 7.6%,

Table 1. Activity of VpAAT1 Recombinant Protein toward Different Acyl-CoAs and Alcohols as Substrates^a

acyl-CoA	alcohol	ester produced	produced in papaya fruit?	AAT activity (pkat mg ⁻¹)
acetyl-CoA	benzyl alcohol	benzyl acetate	no	29275 ± 2593
	geranyl alcohol	geranyl acetate	no	3451 ± 1179
	cinnamyl alcohol	cinnamyl acetate	no	2219 ± 4.9
	phenylethanol	phenethyl acetate	no	805 ± 157
	octanol	octyl acetate	yes	60 ± 15.1
	hexanol	hexyl acetate	yes	20 ± 6.1
	butanol	butyl acetate	yes	1 ± 0.2
	ethanol	ethyl acetate	yes	tr
butanoyl-CoA	butanol	butyl butanoate	yes	526 ± 9.8
	ethanol	ethyl butanoate	yes	83 ± 14.7
hexanoyl-CoA	hexanol	hexyl hexanoate	no	nd
	butanol	butyl hexanoate	yes	50 ± 3.3
	ethanol	ethyl hexanoate	yes	790 ± 147
	methanol	methy hexanoate	yes	4668 ± 1737

^a Calibration curves were prepared for each ester; R^2 values ranged between 1 and 0.93. Data correspond to mean \pm SE. tr, traces; nd, nondetectable.

Table 2. Comparison of AAT Activities toward Different Acyl-CoAs and Alcohol Substrates between VpAAT1 and Closely Related AATs^a

ester produced	Vp AAT1	Cb BEBT	Cm AAT3	Mp AAT1	Cm AAT1 ^b	Ban AAT
benzyl acetate	100	100	100	nr	52	2
methy hexanoate	16	nr	nr	nr	nr	nr
geranyl acetate	12	46	tr	nr	tr	88
cinnamyl acetate	8	8	tr	nr	4	100
phenethyl acetate	3	nr	nd	nr	nd	nr
ethyl hexanoate	3	nr	0	nr	1	nr
butyl butanoate	2	nr	nr	nd	nr	nr
octyl acetate	0	71	nd	nr	5	44
hexyl acetate	0	33	1	100	50	nr
butyl acetate	0	36	3	5	34	1
ethyl acetate	tr	nd	nd	nr	nd	0
ethyl butanoate	0	nr	1	nr	3	nr
hexyl hexanoate	nd	nr	1	85	90	nr
butyl hexanoate	0	nr	2	nd	4	nr

^a The AAT activity of VpAAT1 recombinant protein was assayed by combining a set of three acyl-CoAs (acetyl-, butanoyl-, and hexanoyl-CoA) and nine different alcohols as substrates (ethanol, methanol, butanol, hexanol, octanol, benzyl alcohol, geranyl alcohol, phenylethanol, and cinnamyl alcohol). Some combinations were not quantified. Activity values for related AATs were obtained from the literature (7, 11–13, 29) and expressed as percentage of the maximum activity recorded for each enzyme. tr, traces; nd, nondetected; nr, not reported. ^b 100% activity of CmAAT1 is not mentioned as it corresponds to the production of Z-hexenyl acetate, which was not proved in VpAAT1.

respectively). On the other hand, CmAAT3 and VpAAT1 shared a low activity toward hexyl acetate formation (0.5 and 0.07%, respectively). This analysis could support the hypothesis that members from subfamily III share structural and functional characteristics.

The transcript accumulation pattern provided by qPCR analysis showed that the VpAAT1 gene is expressed exclusively in fruit tissues and that a high level of transcripts are accumulated during ripening of mountain papaya fruit. The increase in VpAAT1 transcripts is coincident with the increase in AAT activity during ripening of the fruit. On the other hand, transcript accumulation of VpAAT1 is induced by ethylene, and its induction is avoided by 1-MCP treatment. The data suggest that the expression of the VpAAT1 gene is modulated by ethylene, as has been reported for other acyltransferases involved in the synthesis of plant volatiles (32). Nevertheless, other regulatory mechanisms besides ethylene could not be discarded (33). The specific transcript accumulation of VpAAT1 in fruit tissue has also been reported previously in other fruit species such as melon (11, 12, 34). Nevertheless, in apple the MpAAT1 gene is expressed not only in ripening fruits but also in flowers and developing fruits (13). On the other hand, genes involved in aroma biosynthesis of floral species such as C. breweri (28) and Rosa hybrida (29) are expressed in their floral organs.

The functionality of VpAAT1 recombinant protein was proved, showing that it was able to use different alcohols and acyl-CoAs as substrates for the synthesis of esters. The assays performed with partially purified enzyme showed a strong activity of the enzyme toward the production of benzyl acetate, which is one of the most powerful odorant compounds used as fragrance in perfumes and foods (35), and it is the main ester produced by AATs belonging to subfamily III (12). We also found a high activity of the recombinant protein toward the formation of esters that are not normally produced by mountain papaya fruit, such as phenethyl acetate and benzyl acetate (Table 1). Similar findings have been reported for the formation of esters in other fruits, regarding the formation of E-2 hexenyl acetate, 2-ethylbutanoate, and 3-methylbutyl, geranyl, and cinnamyl acetate in melon (12) and geranyl, furfuryl, 2-phenylethyl, and benzyl acetate in apple (13). Similarly, SAAT and BanAAT1 displayed a strong preference for the synthesis of geranyl and cinnamyl acetate, respectively, which have not been described in strawberry or banana fruits (7). All together, this could indicate that the volatiles produced by a fruit are determined also by substrate availability and not only AAT selectivity, as has been proposed previously (36-39), albeit AAT purportedly is the ratelimiting step in ester biosynthesis (32).

VpAAT1 protein expressed in yeast was able to produce a wide range of esters, including those normally produced by papaya fruits and some with high aroma impact. This supports the hypothesis that VpAAT1 is involved in aroma biosynthesis in papaya fruit. However, the activity observed toward the formation of these compounds was considerably lower than that toward the synthesis of benzyl acetate, geranyl acetate, cinnamyl acetate, and methyl hexanoate. The reduced activity of VpAAT1 toward the synthesis of butyl acetate and ethyl acetate, compounds that are profusely produced in ripening papaya fruit, most probably indicates that other AAT genes, which have not been described yet, are present in the species.

In conclusion, our study strongly suggests that the VpAATI gene is functional and is involved in the synthesis of esters, which are important contributors to the aroma of papaya fruit. The increase in VpAATI transcripts in fruit tissue during ripening of papaya fruit is coincident with the increment in AAT activity and ester production. Finally, ethylene plays a major role modulating the expression of VpAATI gene and promoting the increment in AAT activity.

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