UNIVERSITAT POLITÈCNICA DE VALÈNCIA

The abscission regulatory module INFLORESCENCE DEFICIENT IN ABSCISSION (IDA) / HAESA (HAE)-like receptor kinases in Solanaceae species: Functional analysis in *Nicotiana benthamiana*

by

Daniel Ventimilla Llora

PhD Supervisors

Dr. Francisco R. Tadeo Serrano

Dr. Manuel Talón Cubillo

Tutor

Dr. María Purificación Lisón Párraga

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FRANCISCO RAMÓN TADEO SERRANO, PhD in Biology and Research Full Professor at the Institut Valencià d'Investigacions Agràries in Montcada (València), and MANUEL TALÓN CUBILLO, PhD in Biology and Research Full Professor at the Institut Valencià d'Investigacions Agràries in Montcada (València).

INFORM:

That the work "The abscission regulatory module INFLORESCENCE DEFICIENT IN ABSCISSION (IDA) / HAESA (HAE)-like receptor kinases in Solanaceae species: Functional analysis in *Nicotiana benthamiana*" has been developed by Daniel Ventimilla Llora under their supervision at the Centre de Genòmica of the Institut Valencià d'Investigacions Agràries, in order to obtain the degree of PhD in Biotechnology at the Universitat Politècnica de València.

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FRANCISCO RAMON|TADEO|SERRANO
Firmado digitalmente por FRANCISCO RAMON|TADEO|SERRANO
Fecha: 2021.03.11 12:51:31 +01'00'

Dr. Francisco Ramón Tadeo Serrano

MANUEL|TALON|CUBILLO
Firmado digitalmente por MANUEL|TALON|CUBILLO
Fecha: 2021.03.11 12:59:47 +01'00'

Dr. Manuel Talón Cubillo

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Table of contents

Abstract

Abscission is an active, organized and highly coordinated cell separation process. Triggering the process of abscission enables the detachment of entire vegetative and reproductive organs, through the modification of cell-to-cell adhesion and breakdown of cell walls at specific sites on the plant body, known as abscission zones (AZs). In *Arabidopsis thaliana* (Arabidopsis), abscission of floral organs and cauline leaves is regulated by the interaction of the hormonal peptide INFLORESCENCE DEFICIENT IN ABSCISSION (IDA), a pair of redundant receptor-like protein kinases, HAESA (HAE) and HAESA-LIKE2 (HSL2), and SOMATIC EMBRYOGENESIS RECEPTOR-LIKE KINASE co-receptors (for recent reviews, see Patharkar and Walker, 2018; Shi et al., 2019). IDA-like peptides, as cell-to-cell communication elements, appear to be involved in other developmental processes that depend on cell separation events such as the emergence of lateral roots (Kumpf et al., 2013; Liu et al., 2018), the sloughing off of the root cap (Shi et al., 2018), or even the responses to biotic and abiotic stresses (Vie et al., 2015, 2017).

In addition to Arabidopsis, *IDA*-like genes have also been identified in a number of crop species. It has been reported that some of them were highly expressed in AZs in tomato (*SlIDA1*; Tucker and Yang, 2012), soybean (*GmIDA2a*; Tucker and Yang, 2012), citrus (*CitIDA3*; Estornell et al., 2015), oil palm (*EgIIDA5*; Stø et al., 2015), litchi (*LcIDL1*; Ying et al., 2016) or yellow lupine (*LlIDA*; Wilmowicz et al., 2018), suggesting that they might conserve the *IDA* function in regulating cell separation during organ abscission. It has been also shown that synthetic IDA peptides are able to induce early floral organ abscission in Arabidopsis flowers (Stenvik et al., 2008), and flower, mature fruit and leaf abscission in yellow lupine, oil palm and Poplar, respectively (Wilmowicz et al., 2018; Tranbarger et al., 2019). Additionally, *IDA* homologs of citrus (*CitIDA3*) and litchi (*LcIDA1*) are functional when heterologously expressed in Arabidopsis, producing earlier floral organ abscission and rescuing the *ida2* abscission deficiency (Estornell et al., 2015; Ying et al., 2016). Similarly, the ectopic over-expression of a *HAE*-like homolog of litchi, *LcHSL2*, completely rescues the abscission of floral organs in the Arabidopsis double mutant *hae hsl2* (Wang et al., 2019a).

Knowledge about the molecular machinery regulating abscission in economically important plant species of the Solanaceae family is currently scarce. In this PhD research, a functional analysis of the components of the abscission signaling module IDA-HAE in *N. benthamiana* was carried out. In the first section of this work, the degree of conservation and the phylogeny of the *IDA*-like and *HAE*-like gene families in relevant species of the genus *Solanum* (tomato, potato and eggplant), *Capsicum* (sweet pepper) and *Nicotiana* (*N. sylvestris*, *N. tomentosiformis*, *N. tabacum* and *N. benthamiana*) were determined.

On the other hand, the expression of these genes in the allopolyploid *N. benthamiana* was analyzed, in order to identify members involved in abscission and in the response to abiotic stress conditions, such as drought. In the second section, the effect of the silencing and over-expression of *NbenIDA1A* and *NbenIDA1B*, two *N. benthamiana IDA*-like homeologs, which were associated with corolla abscission in the previous section, *NbenIDA1A/B*, was evaluated. Furthermore, the effect on corolla abscission of the silencing of the leucine-rich repeat (LRR) receptor-like kinase (RLK), *NbenHAE.1* was also determined.

The results show that the phylogenetic relationships among the *IDA*-like members of the Solanaceae studied, grouped the two pairs of NbenIDA1 and NbenIDA2 protein homeologs with the Arabidopsis prepropeptides related to abscission. Analysis of promoter regions searching for regulatory elements showed that these two pairs of homeologs contained both hormonal and drought response elements, although *NbenIDA2A* lacked the hormonal regulatory elements.

Gene expression analyses also indicate that the pair of *NbenIDA1* homeologs are upregulated during corolla abscission. *NbenIDA1* and *NbenIDA2* pairs showed tissue differential expression under water stress conditions, since *NbenIDA1* homeologs were highly expressed in stressed leaves, while *NbenIDA2* homeologs, especially *NbenIDA2B*, were highly expressed in stressed roots. In non-stressed active growing plants, nodes and internodes were the tissues with the highest expression levels of all members of the *IDA*-like family and their putative *HAE*-like receptors.

VIGS-based silencing of the pair of *NibenIDA1* homeologs and *NbenHAE.1* suppressed corolla abscission in flowers of *N. benthamiana*. This failure in corolla abscission was supported by a blockage in cell wall disassembly at the corolla base, probably due to the lack of upregulation of abscission-related hydrolytic enzymes.

In contrast to the silencing of the pair of *NbenIDA1* homeologs, ectopic over-expression of the homeolog *NbenIDA1A* advanced the timing of both corolla senescence and abscission and negatively affected the growth of *N. benthamiana* plants. Overall, the results obtained using the VIGS approach showed that the pair of *NbenIDA1* homeologs and the *NbenHAE.1* receptor, possibly acting as a signaling module similar to that described in Arabidopsis, regulate corolla abscission in *N. benthamiana* flowers. This is therefore the first example in a plant species other than *Arabidopsis thaliana* that indicates that the IDA-HAE/HSL2 abscission signaling module is conserved in angiosperms.

Resumen

La abscisión es un proceso de separación celular activo, organizado y altamente coordinado. La activación del proceso de abscisión permite el desprendimiento de órganos vegetativos y reproductivos completos, mediante la modificación de la adhesión celular y la desintegración de las paredes celulares en lugares específicos del cuerpo de la planta, conocidos como zonas de abscisión (ZAs). En *Arabidopsis thaliana* (Arabidopsis), la abscisión de órganos florales y hojas caulinares está regulada por la interacción entre el péptido hormonal INFLORESCENCE DEFICIENT IN ABSCISSION (IDA), un par de proteínas quinasas de tipo receptor redundantes, HAESA (HAE) y HAESA-LIKE2 (HSL2) y de correceptores de la familia SOMATIC EMBRYOGENESIS RECEPTOR-LIKE KINASE (véanse revisiones recientes en Patharkar and Walker, 2018; Shi et al., 2019). Los péptidos IDA-like, como elementos de comunicación entre células, parecen estar involucrados en otros procesos de separación celular como la emergencia de raíces laterales de la raíz principal (Kumpf et al., 2013; Liu et al., 2018), el desprendimiento de la caliptra de la raíz (Shi et al., 2018), o incluso las respuestas a estreses bióticos y abióticos (Vie et al., 2015, 2017).

Además de en Arabidopsis, también se han identificado genes *IDA*-like en varias especies de cultivos. Se ha reportado que algunos de ellos presentaban una expresión elevada en ZAs en tomate (*SlIDA1*; Tucker y Yang, 2012), soja (*GmIDA2a*; Tucker y Yang, 2012), cítricos (*CitIDA3*; Estornell et al., 2015), palma aceitera (*EglIDA5*; Stø et al., 2015), litchi (*LcIDL1*; Ying et al., 2016) o lupino amarillo (*LlIDA*; Wilmowicz et al., 2018), lo que sugiere que podrían conservar la función de *IDA* en la regulación de la separación celular durante la abscisión. También se ha demostrado que los péptidos sintéticos IDA son capaces de inducir la abscisión temprana de órganos florales en flores de Arabidopsis (Stenvik et al., 2008), y la abscisión de flores, frutos maduros y hojas en el lupino amarillo, la palma aceitera y el álamo, respectivamente (Wilmowicz et al., 2018; Tranbarger et al., 2019). Además, los homólogos *IDA* de cítricos (*CitIDA3*) y litchi (*LcIDA1*) son funcionales cuando se expresan heterólogamente en Arabidopsis, produciendo una abscisión de órganos florales más temprana y rescatando la deficiencia de abscisión que presenta *ida2* (Estornell et al., 2015; Ying et al., 2016). De manera similar, la sobreexpresión ectópica de un homólogo *HAE*-like de litchi, *LcHSL2*, rescata completamente la abscisión de órganos florales en el mutante doble de Arabidopsis *hae hsl2* (Wang et al., 2019a).

El conocimiento sobre la maquinaria molecular que regula la abscisión en especies de plantas de importancia económica de la familia de las solanáceas es en la actualidad escaso. En esta investigación de doctorado se realizó un análisis funcional de los componentes del módulo de señalización de abscisión IDA-HAE en *N. benthamiana*. En la primera sección de este trabajo, se estudió el grado de conservación y la filogenia de las familias de genes *IDA*-like y *HAE*-like en especies relevantes del género *Solanum* (tomate, patata y berenjena), *Capsicum* (pimiento) y *Nicotiana* (*N. sylvestris, N. tomentosiformis, N. tabacum* y *N. benthamiana*).

Por otro lado, se analizó la expresión de estos genes en el alopoliploide *N. benthamiana*, con el fin de identificar miembros implicados en la abscisión y en la respuesta a condiciones de estrés abiótico, como la sequía. En la segunda sección, se evaluó el efecto del silenciamiento y la sobreexpresión de *NbenIDA1A* y *NbenIDA1B*, dos homeólogos *IDA*-like de *N. benthamiana* que se asociaron con la abscisión de la corola en la sección anterior,

NbenIDA1A/B. Además, también se determinó el efecto sobre la abscisión de la corola del silenciamiento de la quinasa receptor-like (RLK) de repeticiones ricas en leucina (LRR), *NbenHAE.1*.

Los resultados muestran que las relaciones filogenéticas entre los miembros *IDA*-like de las solanáceas estudiadas, agruparon los dos pares de homeólogos de proteínas NbenIDA1 y NbenIDA2 con los prepropéptidos de Arabidopsis relacionados con la abscisión. El análisis de las regiones promotoras en busca de elementos reguladores reveló que estos dos pares de homeólogos contenían elementos de respuesta tanto hormonales como de respuesta a la sequía, aunque *NbenIDA2A* carecía de los elementos reguladores hormonales.

Los análisis de expresión génica también indican que el par de homeólogos *NbenIDA1* se regulan positivamente durante la abscisión de la corola. Los pares *NbenIDA1* y *NbenIDA2* mostraron una expresión diferencial tisular en condiciones de estrés hídrico, ya que los homeólogos *NbenIDA1* se indujeron en hojas estresadas, mientras que los homeólogos *NbenIDA2*, especialmente *NbenIDA2B*, se indujeron en raíces estresadas. En las plantas con crecimiento activo no estresadas, los nudos y los entrenudos fueron los tejidos con los niveles de expresión más altos de todos los miembros de la familia *IDA*-like y sus receptores *HAE*-like putativos.

El silenciamiento basado en VIGS del par de homeólogos *NibenIDA1* y *NbenHAE.1* suprimió la abscisión de la corola en flores de *N. benthamiana*. Este fallo en la abscisión de la corola fue causado por un bloqueo en la desintegración de la pared celular en la base de la corola, probablemente debido a la falta de inducción de las enzimas hidrolíticas relacionadas con la abscisión.

En contraste con el silenciamiento del par de homeólogos *NbenIDA1*, la sobreexpresión ectópica del homeólogo *NbenIDA1A* adelantó la senescencia y la abscisión de la corola y afectó negativamente al crecimiento de las plantas de *N. benthamiana*. En general, los resultados obtenidos utilizando la aproximación VIGS mostraron que el par de homeólogos *NbenIDA1* y el receptor *NbenHAE.1*, posiblemente actuando como un módulo de señalización similar al descrito en Arabidopsis, regulan la abscisión de la corola en las flores de *N. benthamiana*. Este es, por tanto, el primer ejemplo en una especie vegetal distinta de *Arabidopsis thaliana* que indica que el módulo de señalización de abscisión IDA-HAE/HSL2 se conserva en las angiospermas.

Resum

L'abscisió és un procés de separació cel·lular actiu, organitzat i altament coordinat. L'activació del procés d'abscisió permet el despreniment d'òrgans vegetatius i reproductius complets, mitjançant la modificació de l'adhesió cel·lular i la desintegració de les parets cel·lulars en llocs específics del cos de la planta, coneguts com a zones d'abscisió (ZAs). En *Arabidopsis thaliana* (Arabidopsis), l'abscisió d'òrgans florals i fulles caulinars està regulada per la interacció entre el pèptid hormonal INFLORESCENCE DEFICIENT IN ABSCISSION (IDA), un parell de proteïnes cinases de tipus receptor redundants, HAESA (HAE) i HAESA-LIKE2 (HSL2) i de coreceptors de la família SOMATIC EMBRYOGENESIS RECEPTOR-LIKE KINASE (com a revisions recents, consultar Patharkar and Walker, 2018; Shi et al., 2019). Els pèptids IDA-like, com a elements de comunicació entre cèl·lules, semblen estar involucrats en altres processos de separació cel·lular com l'emergència d'arrels laterals de l'arrel principal (Kumpf et al., 2013; Liu et al., 2018), el despreniment de la caliptra de l'arrel (Shi et al., 2018), o fins i tot respostes a estressos biòtics i abiòtics (Vie et al., 2015, 2017).

A més d'en Arabidopsis, també s'han identificat gens *IDA*-like en diverses espècies de cultius. S'ha reportat que alguns d'ells presentaven una expressió elevada en ZAs en tomata (*SlIDA1*; Tucker i Yang, 2012), soia (*GmIDA2a*; Tucker i Yang, 2012), cítrics (*CitIDA3*; Estornell et al., 2015), palma d'oli (*EgIIDA5*; Stø et al., 2015), litxi (*LcIDL1*; Ying et al., 2016) o tramús groc (*LlIDA*; Wilmowicz et al., 2018), el que suggereix que podrien conservar la funció de *IDA* en la regulació de la separació cel·lular durant l'abscisió. També s'ha demostrat que els pèptids sintètics IDA són capaços d'induir l'abscisió primerenca d'òrgans florals en flors d'Arabidopsis (Stenvik et al., 2008), i l'abscisió de flors, fruits madurs i fulles al tramús groc, la palma d'oli i l'àlber, respectivament (Wilmowicz et al., 2018; Tranbarger et al., 2019). A més, els homòlegs *IDA* de cítrics (*CitIDA3*) i litxi (*LcIDA1*) són funcionals quan s'expressen heteròlogament en Arabidopsis, produint una abscisió d'òrgans florals més primerenca i rescatant la deficiència d'abscisió que presenta *ida2* (Estornell et al., 2015; Ying et a l' ., 2016). De manera similar, la sobreexpressió ectòpica d'un homòleg *HAE-like* de litxi, *LcHSL2*, rescata completament l'abscisió d'òrgans florals al mutant doble d'Arabidopsis *hae hsl2* (Wang et al., 2019).

El coneixement sobre la maquinària molecular que regula l'abscisió en espècies de plantes d'importància econòmica de la família de les solanàcies és en la actualitat escàs. En aquesta recerca de doctorat es va realitzar una anàlisi funcional dels components del mòdul de senyalització d'abscisió IDA-HAE en *N. benthamiana*. A la primera secció d'aquest treball, es va estudiar el grau de conservació i la filogènia de les famílies de gens *IDA*-like i *HAE*-like en espècies rellevants del gènere *Solanum* (tomata, creïlla i albergínia), *Capsicum* (pebrot) i *Nicotiana (N. sylvestris, N. tomentosiformis, N. tabacum* i *N. benthamiana*).

D'altra banda, es va analitzar l'expressió d'aquests gens en l'al·lopoliploide *N. benthamiana*, per tal d'identificar membres implicats en l'abscisió i en la resposta a condicions d'estrès abiòtic, com la sequera. A la segona secció, es va avaluar l'efecte del silenciament i la sobreexpressió de *NbenIDA1A* i *NbenIDA1B*, dos homeòlegs *IDA*-like de *N. benthamiana* que es van associar amb l'abscisió de la corol·la a la secció anterior, *NbenIDA1A/B*. A més, també es va determinar l'efecte sobre l'abscisió de la corol·la del silenciament de la cinasa receptor-like (RLK) de repeticions riques en leucina (LRR), *NbenHAE.1*.

Els resultats mostren que les relacions filogenètiques entre els membres *IDA*-like de les solanàcies estudiades van agrupar els dos parells d'homeòlegs de proteïnes NbenIDA1 i NbenIDA2 amb els prepropèptids d'Arabidopsis relacionats amb l'abscisió. L'anàlisi de les regions promotores a la recerca d'elements reguladors va revelar que aquests dos parells d'homeòlegs contenien elements de resposta tan hormonals com de resposta a la sequera, encara que *NbenIDA2A* mancava dels elements reguladors hormonals.

Les anàlisis d'expressió gènica també indiquen que el parell d'homeòlegs *NbenIDA1* es regulen positivament durant l'abscisió de la corol·la. Els parells *NbenIDA1* i *NbenIDA2* van mostrar una expressió diferencial tissular en condicions d'estrès hídric, ja que els homeòlegs *NbenIDA1* es van induir en fulles estressades, mentre que els homeòlegs *NbenIDA2*, especialment *NbenIDA2B*, es van induir en arrels estressades. A les plantes amb creixement actiu no estressades, els nusos i els entrenusos van ser els teixits amb els nivells d'expressió més alts de tots els membres de la família *IDA-like* i els seus receptors *HAE-like* putatius.

El silenciament basat en VIGS del parell d'homeòlegs *NibenIDA1* i *NbenHAE.1* va suprimir l'abscisió de la corol·la en flors de *N. benthamiana*. Aquesta errada a l'abscisió de la corol·la va ser causada per un bloqueig en la desintegració de la paret cel·lular a la base de la corol·la, probablement degut a la manca d'inducció dels enzims hidrolítics relacionades amb l'abscisió.

En contrast amb el silenciament del parell d'homeòlegs *NbenIDA1*, la sobreexpressió ectòpica de l'homeòleg *NbenIDA1A* va avançar la senescència i l'abscisió de la corol·la i va afectar negativament el creixement de les plantes de *N. benthamiana*. En general, els resultats obtinguts utilitzant l'aproximació VIGS van mostrar que el parell d'homeòlegs *NbenIDA1* i el receptor *NbenHAE.1*, possiblement actuant com un mòdul de senyalització similar al descrit en Arabidopsis, regulen l'abscisió de la corol·la en les flors de *N. benthamiana*. Aquest és, per tant, el primer exemple en una espècie vegetal diferent d'*Arabidopsis thaliana* que indica que el mòdul de senyalització d'abscisió IDA-HAE/HSL2 es conserva en les angiospermes.

Abbreviations

5’-UTR	Five prime untranslated region
α-AFase	α-arabinofuranosidase
β-GAL	β-galactosidase
AB	apical bud
ABA	abscisic acid
ACC	1-aminocyclopropane-1-carboxylic acid
ACO	1-aminocyclopropane-1-carboxylic acid oxidase
ACS	1-aminocyclopropane-1-carboxylate synthase
ADP	adenosine diphosphate
An2	anthers at stage 2
An4	anthers at stage 4
AP2/ERF	APETALA 2/ethylene response factor
ARF	auxin response factor
ATP	adenosine triphosphate
AUX	auxins
Aux/IAA	auxin/indole-3-acetic acid
AZ	abscission zone
AZ-C	abscission zone C (citrus fruit)
bHLH	basic helix-loop-helix
BA	benzyladenine
BiFC	bimolecular fluorescence complementation
BLAST	Basic Local Alignment Sequence Tool
bp	base pairs
BR	brassinosteroids
cBS	corolla breakstrength
CCD	corolla cell death
cDNA	complementary deoxyribonucleic acid
CDS	coding sequence
CEL	endo-β-1,4-glucanases/cellulase
CK	cytokinins
CLBV	*Citrus leaf blotch virus*
CMNP	5-chloro-3-methyl-4-nitro-1*H*-pyrazole
Co	corolla
CP	capsid protein

Ct	cycle threshold
CWR	cell wall remodeling enzymes and modifying proteins
DDBJ	DNA Data Bank of Japan
DNA	deoxyribonucleic acid
DOF	DNA binding with one finger
EPIP	extended PIP
ERF	ethylene response factor
EXP	expansin
FC	fold change
Fr2	fruit at stage 2
Fr4	fruit at stage 4
GA1	gibberellin A1
GA_3	gibberellic acid
GAs	gibberellins
gf	gram-force
GFP	green fluorescent protein
GTP	guanosine-5'-triphosphate
HAE	HAESA
HG	homogalacturonan
HSL2	HAESA-like 2
IAA	indole-3-acetic acid
IDA	INFLORESCENCE DEFICIENT IN ABSCISSION
IDL	INFLORESCENCE DEFFICIENT IN ABSCISSON-like
In	internodes
IVIA	Instituto Valenciano de Investigaciones Agrarias
JA	jasmonic acid
LAC	laccase
LAZ	laminar abscission zone
LRR-RLK	leucine-rich repeat receptor-like protein kinase
MAPK	mitogen-activated protein kinase
MEGA	Molecular Evolutionary Genetics Analysis
MeJa	methyl jasmonate
MKK	mitogen-activated protein kinase kinase
ML	mature leaf
MPK6	mitogen-activated protein kinase 6

mRNA	messenger ribonucleic acid
N	nodes
PA	polyamine
PAE	pectin acetylesterase
pBS	petal breakstrength
PCD	programmed cell death
PCR	polymerase chain reaction
PER	peroxidase
PG	polygalacturonase
PL	pectate lyase
PME	pectin methylesterase
PMEI	pectin methylesterase inhibitor
PR	pathogenesis-related
qPCR	quantitative polymerase chain reaction
R	roots
RG	rhamnogalacturonan
RNA	ribonucleic acid
RNase	Ribonuclease
ROS	reactive oxygen species
SA	salicylic acid
SAM	shoot apical meristem
S+S	style and stigma
SERK	Somatic embryogenesis receptor kinase
SGN	Solanaceae Genomics Network
TAIR	The Arabidopsis Information Resource
TRV	tobacco rattle virus
US	United States
VIGS	virus-induced gene silencing
WT	wild type
XTH	xyloglucan endotransglucosylase/hydrolase
YL	young leaf

1
General introduction

1.1. Intercellular adhesion and cell separation are key processes for plant growth and development

The cell wall surrounding plant cells is one of the defining features of the plant kingdom (Keegstra, 2010). The main function of the cell wall is to provide the cell with the necessary rigidity to resist internal turgor pressure and thus prevent cells from exploding, but cell walls must also be flexible enough to direct cell expansion. The cell wall provides the basic structural backbone serving as the mechanical support for forming the tissues and organs of a plant and, by being on the surface of cells, also protects against pathogen attack. In addition, cell walls also play an important role in cell-to-cell communication and in cell proliferation and adhesion (Tsang et al., 2010).

The functional specialization of tissues and organs is determined by cell wall composition, resulting in a specialized cell wall spectrum with primary and secondary walls located at both ends of that spectrum (De Lorenzo et al., 2019). The major components (>90%) of plant cell walls are polysaccharides forming a mesh of cellulose microfibrils cross-linked to each other by branched polysaccharides, hemicelluloses and pectins (Albersheim et al., 1996). Cellulose is a water insoluble linear polymer of β-(1,4)-D-glucose residues making up long and rigid microfibrils. Those cellulose microfibrils associate between them in a parallel orientation by hydrogen bonding and Van der Waals forces (Nishiyama et al., 2002) forming sheet-like structures (Somerville, 2006). The fibrous structure of cellulose enables the maintenance of structural integrity of both primary and secondary cell walls.

The most common hemicelluloses in cell walls are xyloglucans and xylans. The xyloglucan backbone is composed of β-(1,4)-linked D-glucose residues that have α-(1,6)-linked xylosyl side chains. These side chains in turn can be further decorated with L-arabinose, D-xylose, and, less frequently, L-fucose residues, to create complex levels of branches and patterns. The backbone of xylan is composed of β-(1,4)-linked D-xylose residues which can be decorated with D-glucuronic acid to produce glucuroxylan (Pauly et al., 2013). Xyloglucans are the main hemicellulose in the primary walls of dicot plants while xylans are in the secondary cell walls.

Pectins are a complex class of cell wall polysaccharides including homogalacturonan (HG), rhamnogalacturonan-I (RG-I), and rhamnogalacturonan-II (RG-II) (Figure 1.1). HGs and RG-II have backbones consisting of α-(1,4)-D-galacturonic acid whereas RG-I consists of a repeated motif of α-(1,4)-D-galacturonic acid and α-(1,2)-L-rhamnose (Caffal and Mohnen, 2009). The backbone of RG-I is decorated with L-arabinose and D-galactose, and that of RG-II with complex heteropolysaccharides. Once synthesized in the Golgi, HGs are transported to the wall in highly esterified forms carrying methyl groups at the C-6 carboxyl or acetyl groups at the O-2 or O-3 of the galacturonic acid residues, although they become later selectively de-methyl esterified and de-acetylated (Caffall and Mohnen, 2009). When several consecutive D-galacturonic acid residues are de-methyl esterified and de-acetylated, then the negatively charged carboxyl groups can form calcium bonds with other HGs, leading to so-called 'egg-box' structures underlying the formation of pectin gels (Li et al., 2007). The calcium cross-linked HGs are critical for tissue integrity, wall plasticity and cell adhesion (Willats et al., 2001; Ezaki et al., 2005; Derbyshire et al., 2007). De-methyl esterified and de-acetylated calcium cross-linked HGs increase the amount of bound water maintaining wall hydration (White et al., 2014), and the hydration state is shown to affect the rigidity of the cell wall (Ha et al., 1997). In addition, the strength of pectin gels is highly dependent on the amount of free calcium ions in the apoplast, as stiffness of the gel is reduced by disassociation of calcium crosslinks (Tibbits et al., 1998). On the other hand, partially de-methyl esterified and de-acetylated HGs can become a target for pectin-degrading enzymes (Lionetti et al., 2015).

1.1.1. Plant cells are attached to their neighbors by a shared cell wall interface, the middle lamella

The integrity of multicellular organisms depends upon the establishment and maintenance of stable cellular connections (Abedin and King, 2010). Cell adhesion in plant tissues occurs through the cell wall and primarily at the level of middle lamella. The middle lamella is an adhesive matrix composed mainly of pectic polysaccharides (Zamil and Geitmann, 2017). In most cases, structures formed by adhesion between cells are maintained throughout the whole life cycle of a plant, although effective separation of contiguous cells is crucial at some plant developmental stages and in certain environmental scenarios (Roberts et al., 2000; Daher and Braybrook, 2015).

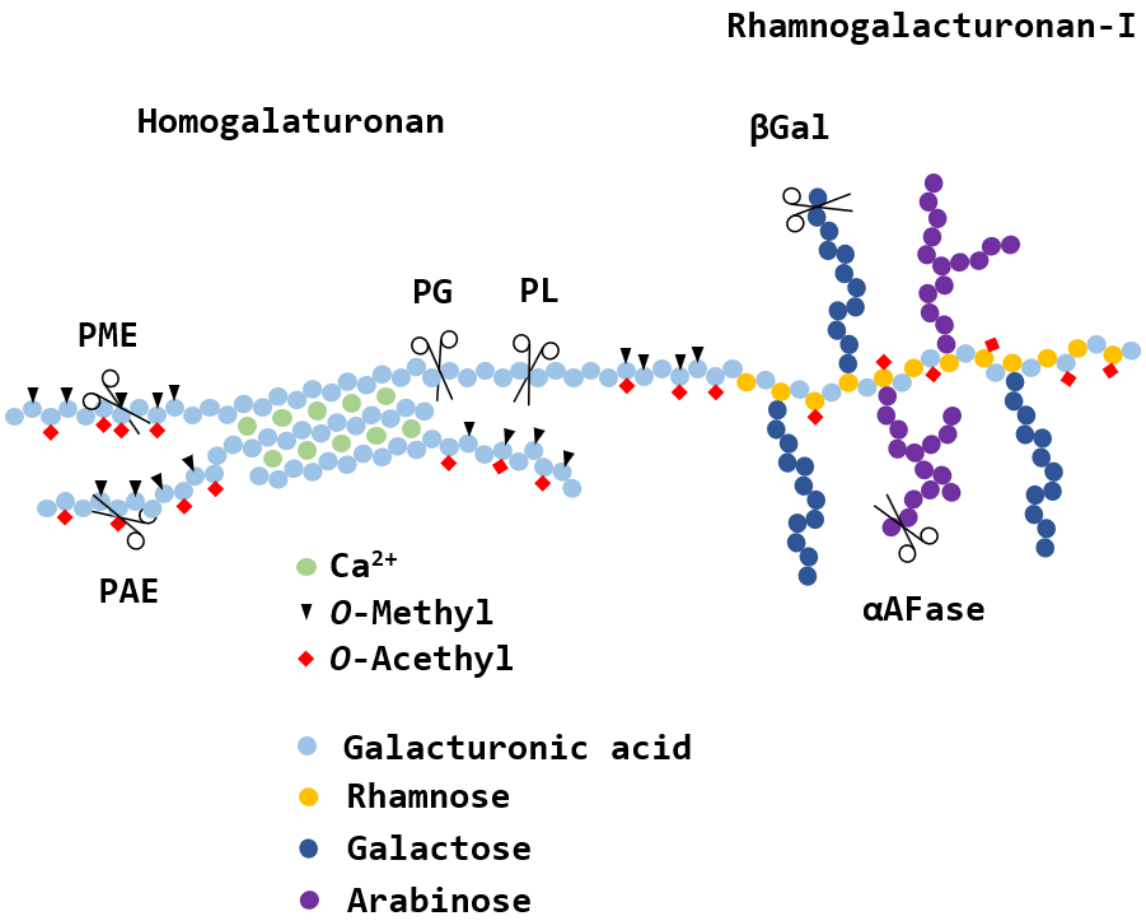

Figure 1.1. Diagrammatic structures of pectin polysaccharides homogalacturonan and rhamnogalacturonan-I. Noncovalent calcium-mediated interactions between carboxyl groups of de-methyl esterified and de-acetylated HGs can create an 'egg-box' structure that promotes gel formation affecting the rigidity of cell walls. Degradation of partially de-methyl esterified and de-acetylated pectic polymers occurs as a result of the action of several cell wall-remodeling enzymes: pectin-methylesterase (PME), pectin-acetylesterase (PAE), polygalacturonase (PG), pectate-lyase (PL), β-galactosidase (β-GAL) and α-arabinofuranosidase (α-AFase).

1.1.2. Molecular determinants associated with cell adhesion

The establishment and maintenance of cell-to-cell adhesion is associated with chemical modifications of the pectins that make up the middle lamella as they affect its ability to gel and act as a glue between cells (Daher and Braybrook, 2015). Homogalacturonans are gelled by calcium-mediated cross-linking and this occurs in regions with low esterification levels such as the corners of the intercellular spaces and the middle lamella (Jarvis et al., 2003). When released into extracellular space and integrated into the cell wall, the HGs are highly methyl-esterified and acetylated. Methyl esterification and acetylation of HG correlates negatively with cell adhesion because it interferes with the binding of calcium to galacturonic acid and the formation of 'egg box' domains (Ralet et al., 2003). It is the activity of specific enzymes that modify the cell walls, the pectin methylesterases (PMEs) and the pectin acetylesterases (PAEs), which eliminate, respectively, the methyl and acetyl groups of the HGs (Micheli, 2001; Willats et al., 2001; Peaucelle et al., 2011; Braybrook et al., 2012; Philippe et al., 2017). A balance between the activity of PMEs and that of another group of cell wall enzymes, pectin-

methylesterase inhibitors (PMEIs), determines the cohesive properties of the middle lamella. Inhibition of PME activity through the transient overexpression of *AtPMEI3* was found to cause failures in the proper separation of the inflorescences from the main stem (Müller et al., 2013). The role in intercellular adhesion of the other two pectic polysaccharides, RG-Is and RG-IIs, is controversial as mutants for both tobacco and *Arabidopsis thaliana* show conflicting results (Iwai et al., 2002; Gendre et al., 2013). The de-esterified forms of HGs are found in the middle lamella and in the corners of the cell junctions, which refers the cell-to-cell adhesion features to these specific tissue locations.

1.2. Loss of intercellular adhesion leads to cell separation

Intercellular adhesion is lost in certain developmental processes and then cell separation occurs. The emergence of primary and secondary roots and their penetration into the soil, the expansion of cotyledons and leaves, the formation of stomata and intercellular air spaces, the dispersion of pollen from the anthers, the softening of fleshy fruits during ripening, the dehiscence of pods/siliques and the detachment of plant organs require the activation of cell separation (Roberts et al., 2002). Since cell separation is a process involving the loss of cell adhesion, then it must be associated with alterations in HGs. There are several examples in the literature that involve PMEs and polygalacturonases (PGs) in the development of cell separation processes. Inhibition of PME activity prevents the sloughing off of the root cap (Wen et al., 1999), and in two mutants of Arabidopsis, *qrt1* (*QUARTET1*, a PME) and *qrt3* (*QUARTET3*, a PG), there is a failure in the separation of microspores that remain united in a tetrahedral cluster of four pollen grains (Rhee et al., 2003; Francis et al., 2006). Thus, both activities seem to be necessary to separate the microspores: the PME that eliminates the methyl groups from the HG, and subsequently the PG activity degrading the HG and then releasing the pollen grains. In addition to their role in the separation of microspores, PGs have also been implicated in other cell separation processes such as pod/silique dehiscence and organ abscission. Degradation of HG by the endo-PG ARABIDOPSIS DEHISCENCE ZONE POLYGALACTURONASE2 (ADPG2) and QUARTET2 (QRT2) is required to enable the separation of valves from the replum in the silique of *Arabidopsis thaliana* to allow pod shattering upon maturity (González-Carranza et al., 2002, 2007; Ogawa et al., 2009). In addition, *adpg2/qrt2* double mutant plants have a delayed abscission phenotype (Ogawa et al., 2009), which provides functional evidence that these PGs have a role in pod dehiscence and organ abscission. Since pod development is accompanied by an increase in PME activity (Louvet et al., 2011), HG degradation appears to be PME-dependent and PG-mediated. The key role of PGs in the loss of cell adhesion is supported by over-expression and silencing studies conducted, respectively, in apple (Atkinson et al., 2012) and tomato (Jiang et al., 2008). The degradation of HGs is also caused by the activity of pectate lyases (Marín-Rodríguez et al., 2002). Fruit peeling is a process associated with the loss of cell adhesion between the peel and the pulp in certain fruit species such as banana (*Musa acuminata*) during the ripening of the fruit. The separation of the peel from the pulp occurs along the loculus, the inner face of the peel where the vascular bundles are located (Kheng et al., 2011). Pectin solubilization occurred to a greater extent in the cell walls of the banana fruit pulp and correlated with increases in expression of two ripening-related pectate lyase genes (Marín-Rodríguez et al., 2003). In another cell separation process such as abscission, pectate lyases have also been linked to pectin dissolution in the middle lamella of AZ cells which probably contributes to organ shedding (Lashbrook and Cai, 2008; Sun and van Nocker, 2010; Singh et al., 2011; Merelo et al., 2017).

1.3. Abscission is a cell separation process

Abscission is a highly coordinated process of cell separation involving the natural detachment of plant tissues and organs from the parent plant. It is a universal process since it occurs in all higher plants and, thanks to its activation, they can detach from various aerial structures such as seeds and fruits, thus ensuring an efficient propagation of the species. In addition, it allows the shedding of senescent or non-functional organs as well as damaged or infected organs (for a review, see Estornell et al., 2013). However, from an agronomic point of view, abscission can be a disadvantage as it has a direct impact on crop yield.

1.3.1. Abscission is regulated by developmental and environmental cues

It is a well-known and established concept that abscission is triggered by physiological factors related to senescence, environmental factors associated with stress, and hormonal factors as well. These factors may act independently or in close association but, in any case, it is not known whether the signals inducing the abscission of the different plant organs are the same or not.

1.3.1.1. Physiological factors

Abscission is often related to senescence since both processes are triggered, in many cases, by the same factors. However, senescence leads to the aging or death of an organ or part of it, while abscission occurs as a consequence of this degradation and to eliminate the organ (Taylor and Whitelaw, 2001). These are two independent physiological processes that may or may not be coupled, since under certain circumstances abscission may occur without senescence and vice versa. A clear example of activated abscission because of organ senescence is that of autumnal leaf fall: once the photosynthetic rate drops below a certain level, leaf senescence and abscission follow one another in an orderly fashion to prevent a situation where water and nutrient consumption exceeds the contribution of fixed carbon (Batt and Woolhouse, 1975; Hensel et al., 1993).

1.3.1.2. Environmental factors

A reduction in the photoperiod has been identified as a signal that activates a switch between the expression of genes encoding enzymes required for photosynthesis and that of proteins related to senescence and abscission (Taylor and Whitelaw, 2001). Several studies carried out in *Coleus blumei* (Mao et al., 1989), *Capsicum annum* (Wien et al., 1989) and *Lilium* (Van Meeteren and De Proft, 1982) confirm that dark and low light conditions promote abscission of flowers, flower buds, leaves and fruits. Shading of soybean plants (*Glycine max*) reduces the photosynthetic rate and activates senescence and leaf abscission (Burkey and Wells, 1991), while it induces abscission of immature fruits in apple (*Malus domestica*) and grape (*Vitis vinifera*) mainly by reducing carbohydrate metabolism (Zhou et al., 2008; Domingos et al., 2015).

Extreme temperatures can also trigger organ abscission. High temperatures cause flower abscission in pepper (*Capsicum annum*) and also in pea (*Pisum sativum,* Guilioni, 1997; González-Dugo et al., 2007), while low temperatures promote fruit drop in the ornamental plant

Amur honeysuckle *(Lonicera maacki,* Bartuszevige et al., 2006) and subfreezing temperatures promote leaf abscission in citrus trees (Young and Meredith, 1971).

Drought conditions and other stresses that cause water deficit, such as salinity and extreme temperatures, promote abscission in a high number of species. Leaf abscission due to water stress is a common occurrence in deciduous species that grow in tropical and subtropical climates (e.g. species of the genus *Spondias*), and is necessary to reduce the speed of transpiration and competition for light (Addicott, 1982). This phenomenon is known as 'hygrophobic leaf abscission' and is also evident in species undergoing leaf abscission in wet periods after a period of drought, as occurs in areas with Mediterranean climate. Leaf abscission during rehydration after a period of water stress has also been observed in cotton and citrus plants (Jordan et al., 1972; Tudela and Primo-Millo, 1992), and recently in cauline leaves in *Arabidopsis thaliana* (Patharkar and Walker, 2016).

Injuries and pathogen attack must be considered together because they produce the same type of stimulus in the plant. Mechanical damage is a possible entry point for pathogens, so the plant induces a defense response that leads to a significant alteration of gene expression. The main purpose of the defensive response is to heal the wound and prevent pathogenic invasion. This is achieved by strengthening the cell wall by deposition of callose, lignin and hydroxyprotein-rich glycoproteins, and by the synthesis of antimicrobial compounds such as phytoalexins, proteinase inhibitors and pathogen response proteins. If this type of defensive response is not activated, pathogenic invasion occurs and plants then respond differently, shedding the infected organ to prevent the spread of infection (Taylor and Whitelaw, 2001).

All the adverse environmental conditions mentioned above interfere with carbon assimilation and/or respiration causing energy deprivation (Baena-González and Sheen, 2008) and triggering organ abscission. Competition for photoassimilates between actively growing organs imposes nutritional stress and energy deficit conditions, generally ending in cessation of organ growth and activation of abscission. In citrus trees, manipulation of the sugar supply available for developing fruits through defoliation, stimulates bud sprouting, thus increasing the competition for carbohydrates between shoots and fruits and triggering fruit abscission (Gómez-Cadenas et al., 2000).

1.3.1.3. Hormonal factors

In a general sense, ethylene, abscisic acid (ABA), jasmonic acid and in specific circumstances cytokinins, act as abscission-accelerating factors, while auxin, gibberellins, polyamines and brassinosteroids as abscission-inhibiting factors (Taylor and Whitelaw, 2001; Estornell et al., 2013).

Ethylene plays an important role as a positive regulator of abscission as it accelerates senescence and increases its emission by plant tissues under environmental stress (Jackson and Osborne, 1970; Brown, 1997). Ethylene treatment increases abscission of leaves, flowers, and fruits whereas treatments with inhibitors of ethylene biosynthesis delay abscission. Ethylene activates the expression of genes encoding cell wall remodeling enzymes and their secretion to cell walls (Addicott, 1982; Sexton and Roberts, 1982; del Campillo and Bennett, 1996; Brummell et al., 1999; Lashbrook and Cai, 2008; Sundaresan et al., 2016; Merelo et al., 2017). However, studies in Arabidopsis mutants lacking ethylene perception (*etr1-1*) and

signaling (*ein2-1*) have suggested that ethylene may only play a subsidiary role in determining the timing of the onset of abscission, while it may not be essential for its activation. In tomato, reduction in the expression of *LeETR1* (Whitelaw et al., 2002) or mutations affecting ethylene perception and sensitivity such as *Never ripe* (*Nr*) and *Sletr1-1* and *Sletr1-2* (Lanahan et al., 1994; Okabe et al., 2011) delayed organ abscission. Seedlings of the *Nr* mutant respond to low concentrations of ethylene (1 ppm, Lanahan et al., 1994) while those of the *Sletr1-1* mutant show no response to 10 ppm of ethylene (Okabe et al., 2011), suggesting that ethylene insensitivity in *Sletr1-1* resembles that of Arabidopsis *etr1-1* mutant, a completely ethylene insensitive mutation. An ethylene-independent pathway participating in the regulation of organ abscission has been proposed in Arabidopsis (Bleecker and Patterson, 1997), and several delayed abscission mutants (*dab*) that exhibit normal response to ethylene have been identified (Patterson and Bleecker, 2004). This abscission regulatory ethylene-independent pathway could be operative in tomato as well: it has been suggested that ethylene effect on gene expression may be tissue-dependent (Lincoln et al., 1987; Riechmann and Meyerowitz, 1998). Moreover, it cannot be ruled out that the ethylene effect on floral abscission could be carried out by abscission-specific proteins other than class I ethylene receptors and EIN2 rather than by intermediaries from an ethylene-independent pathway. All relevant data collected in the literature on organ abscission suggest that ethylene plays a major role in the initiation and progression of abscission (Estornell et al., 2013; Sawicki et al., 2015; Botton and Ruperti, 2019).

The role of ABA was initially related to abscission, but now it is mostly associated with its ability to trigger tissue senescence. The effect of ABA on abscission seems to depend on interactions with auxin or ethylene rather than being a direct effect of ABA (Patterson, 2001; Roberts et al., 2002). Thus, while ethylene appears to be the final hormonal activator of abscission, ABA, like auxin, could have an intermediate role (Zacarias et al., 1995; Gomez-Cadenas et al., 1996, 2000; Agustí et al., 2007). ABA together with jasmonate is required to activate the expression of some cell wall-modifying enzymes during abscission in Arabidopsis hormone-insensitive mutants (Ogawa et al., 2009).

Cytokinins are implicated in the regulation of cell division and expansion, intervening in many physiological processes. Although high concentration of cytokinins has been shown to inhibit abscission (Pierik and Abbadi, 1972), its effect on abscission is rather related to the promotion of the process. In fact, some synthetic cytokinin-like compounds induce abscission and are used as defoliants. However, it is thought that cytokinin action on abscission is mediated by ethylene (Sipes and Einset, 1983; Grossmann, 1991; Dal Cin et al., 2007). In apple trees, canopy treatment with the cytokinin benzyladenine (BA) increases abscission of young fruits probably by exacerbating competition between shoots and fruit clusters, due to stimulation of vegetative growth (Dal Cin et al., 2007). Treatment with BA induces the expression of ethylene biosynthetic genes (mainly ACC oxidase, *MdACO1*) and a transient increase in ethylene emission in young fruits with a high probability to abscise (Dal Cin et al., 2007; Botton et al., 2011).

Jasmonic acid is traditionally associated with the regulation of pathogens response. Although treatment with jasmonate accelerates abscission (Staswick et al., 1995), this is a general stress response that ultimately triggers ethylene production (Taylor and Whitelaw, 2001). Conversely, some studies suggest a more direct role of jasmonate in the activation of abscission other than that of setting up a defense response (Ueda et al., 1996; Miyamoto et al., 1997; Hartmond et al., 2000; Beno-Moualem et al., 2004; Agustí et al., 2008; Vashisth and Malladi, 2014; Vashisth et al., 2015).

The current understanding of the hormonal mechanisms that establish the timing and progression of organ abscission is based on early data showing a positive correlation between organ senescence, organ auxin levels and abscission (Addicott, 1982). It was observed that the application of auxin at the distal end of AZ explants delayed abscission, whereas if applied at the proximal end, it accelerated it (Addicott and Lynch, 1951), suggesting that changes in auxin gradients may signal the onset of senescence and abscission (Addicott et al., 1955). In addition, the interaction of auxin with other hormones, notably with ethylene, has also been demonstrated (see Sexton and Roberts, 1982; Taylor and Whitelaw, 2001). At present, it is generally accepted that the basipetal polar flux of auxin from the distal portion toward the site where organ detachment will occur, makes it insensitive to ethylene, delaying or preventing abscission. Conversely, if the basipetal polar flow of auxin is blocked, the insensitivity to ethylene disappears and abscission is activated. Genetic and molecular data support a role of auxin biosynthesis and signaling in inhibiting organ abscission (Ellis et al., 2005; Okushima et al., 2005; Meir et al., 2006; Basu et al., 2013; Shi et al., 2017; Fu et al., 2019).

Although it was initially reported that the application of gibberellic acid (GA_3) accelerated organ abscission in explants of coleus, bean and cotton seedlings (Rosen and Siegel, 1963; Chatterjee and Leopold, 1964; Lyon and Smith, 1966), the 3β-hydroxylated gibberellins produced endogenously by developing ovaries are essential to avoid early abscission by promoting fruit set in fruit tree crops (Talon et al., 1992; Ben-Cheikh et al., 1997; Kojima et al., 1999; Reig et al., 2018). Additionally, it has been reported that application of gibberellins (GAs) improved fruit set in citrus, persimmon and pear (Talon et al., 1992; Reig et al., 2018; Lordan et al., 2019). Therefore, GAs seem to be abscission-inhibiting hormonal factors.

The role of polyamines (PAs) in abscission may be associated with their activity in delaying plant senescence (Wang et al., 2019b). PAs are apparently involved in grape berry abscission (Aziz et al., 2001) and, in addition, treatments with an arginine decarboxylase inhibitor reduced putrescine concentrations and stimulated mango fruitlet abscission (Malik and Singh, 2003) and also mature olive fruit abscission (Gomez-Jimenez et al., 2010; Gil-Amado and Gomez-Jimenez, 2012). The involvement of PAs in the regulation of mature olive fruit abscission was partly associated with the downregulation of ethylene biosynthesis and signaling genes (Parra-Lobato and Gomez-Jimenez, 2011). In excised tobacco (*Nicotiana tabacum*) flowers, exogenous spermine (a type of PA) delayed senescence and corolla cell death (CCD) and caused an increase in free and acid-soluble conjugated PA levels (Serafini-Fracassini et al., 2002). This delay of CCD by PAs, together with the observation that CCD was preceded by the stimulation of transaminase activity, which is involved in the conjugation of PAs with proteins (Della Mea et al., 2007), support the notion that PAs would have a repressive effect on the evolution of senescence and, therefore, on corolla abscission in tobacco flowers.

Brassinosteroids have also been involved in the regulation of the timing of plant senescence (Karlova and de Vries, 2006) and, as mentioned above for PAs, this effect may be related to their activity in delaying organ abscission. Applications of epi-brassinolide delayed organ senescence and abscission of citrus leaf and fruitlet explants (Iwahori et al., 1990) and increased fruit set in grapes (Tadayon and Moafpourian, 2019).

Knowledge about the role of hormones in organ abscission has directed attention to the use of abscission-triggering chemicals as a harvest management practice to improve the efficiency of mechanical harvesting and minimize tree damage during harvesting. The ethylene releasing compound ethephon (2-chloroethyl phosphonic acid), alone or in combination with other chemicals, is used to reduce the detachment force of fruit and promote mechanical harvesting in various fruit tree crops (as examples, see Bukovac, 1979; Ferrara et al., 2016 and Goldental-Cohen et al., 2017). Ethephon increased both the expression of two ethylene biosynthesis genes, *CsACS1* and *CsACO* in AZs, thus triggering citrus leaf and fruit abscission (Yuan et al., 2005). The combined treatment with ethephon and guanfacine or clonidine, two G-protein-coupled α_{2A}-adrenoreceptor selective agonists, reduced ethephon-enhanced expression of *CsACS1* and *CsACO* in the laminar AZ and leaf abscission. Therefore, the observed effects on leaf abscission strongly suggest a link between G-protein-related signaling, ethylene biosynthesis and organ abscission. The abscission-triggering chemical CMNP (5-chloro-3-methyl-4-nitro-1*H*-pyrazole) is the only one that selectively loosens citrus mature fruit. The application of CMNP stimulated citrus fruit abscission and this effect was associated with energy deprivation and changes in hormone homeostasis (Yuan et al., 2001). The canopy treatment with CMNP caused, in addition to fruit abscission, fruit peel injury and stimulation of wound ethylene production (Yuan et al., 2001). Furthermore, CMNP was highly effective reducing the attachment force of the fruit to the AZ when the auxin to ABA balance in fruit peel was low (Yuan et al., 2001). CMNP acts as an uncoupler, disrupting phosphorylation in mitochondria and chloroplast and reducing ATP content in citrus fruit peel (Alférez et al., 2005). In Arabidopsis leaves, CMNP upregulated genes associated with stress, lipid signaling and also cell energetics (trehalose-6-phosphate synthase), and other genes related to anoxia, senescence, and detoxification (Alférez et al., 2007).

1.3.2. The abscission pathway involves four sequential stages

The currently accepted model describing the development of the abscission process was proposed by Patterson (2001) and includes four major sequential stages (Figure 1.2):

a) differentiation of an abscission zone at the future location of organ detachment
b) acquisition by the abscission zone cells of competence to respond to abscission-promoting cues
c) activation of the cell separation process within the abscission zone and organ detachment
d) post-abscission differentiation of a protective layer on the surface of the separation layer at the main body of the plant

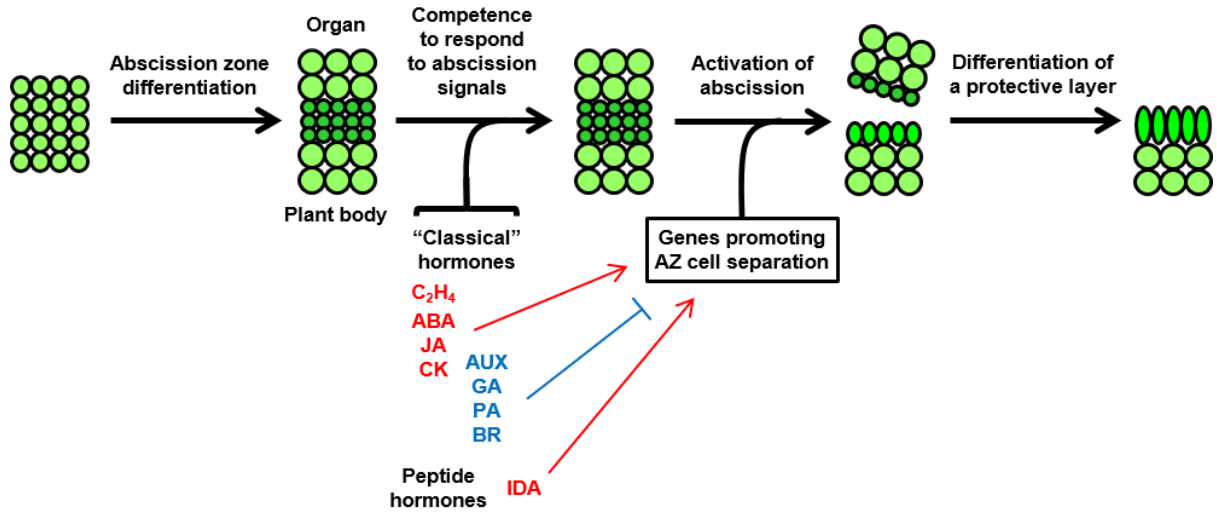

Figure 1.2. The commonly accepted model of organ abscission defines four major steps in the abscission pathway. The first step is related to the differentiation of functional AZs (small dark green circles), that can be positioned either at the boundary between organs (e.g., at the base of floral organs and the receptacle, and at the junction between the ovule/seed and the funiculus in Arabidopsis, or at the base of the rice grain) or within an organ (e.g., in the flower pedicel of tomato or in the tobacco corolla). Once the AZ is properly differentiated, AZ cells must acquire competence to respond to developmental and environmental signals. The response of AZ cells to internal and external triggering-abscission signals may be mediated by the balance between "classical" hormones and by the action of particular peptide hormones. These abscission agents regulate abscission by modulating the expression of abscission-related genes during the third step of organ abscission associated with the activation of cell wall loosening in the separation layer within the AZ and the execution of organ detachment. The last step of organ abscission is the differentiation of a protective layer on the surface of the proximal separation layer. This protective layer might serve for at least two purposes: to act as a barrier against uncontrolled water loss and to protect the plant from pathogen aggression (Adapted from Estornell et al., 2013).

1.3.2.1. Differentiation of the abscission zone

The first stage of the abscission pathway involves the ontogeny of the tissue where cell separation will occur, the abscission zone (AZ). The cells in an AZ are clearly distinguishable both morphologically and anatomically from their neighboring cells as they are smaller, with dense cytoplasm and are interconnected by plasmodesmata (Addicott, 1982; Sexton and Roberts, 1982; Osborne and Morgan, 1989). The number of cell layers of the AZ is highly variable, ranging from a single layer of cells as in the AZ located at the junction between the petiole and the pulvinus within the primary leaf of common bean (Wright and Osborne, 1974), to 20-30 cell layers in the leaflet AZ of elderberry (Osborne and Sargent, 1976). The physiological processes leading to cell separation within multilayered AZs are restricted to a narrow band of cells known as the separation layer (Addicott, 1982).

Two types of AZs have been described: primary AZs and adventitious or secondary AZs. Differentiation of primary AZs takes place very early and simultaneously with the development of lateral organs formed from the shoot apical meristem (SAM) (Addicott, 1982; Sexton and Roberts, 1982; Osborne and Morgan, 1989; Taylor and Whitelaw, 2001; Roberts et al., 2002; Estornell et al., 2013; Tranbarger and Tadeo, 2020). Primary AZs are formed in well-defined positions on the plant body, usually at the boundary between the future shed organ and the plant body. However, there are exceptions to this AZ location at organ boundaries, such as those located at the proximal end within the flower pedicel of tomato (Szymkowiak and Irish, 1999). Abscission of floral organs, flowers, fruits, seeds and leaves occurs by activation of primary AZs. On the other hand, differentiation of adventitious or secondary AZs takes place after the development of lateral organs in a position that is not predetermined by plant architecture (Addicott, 1982). Examples of such adventitious AZs are found during natural abscission of the flower style or spring buds (Goldschmidt and Leshem, 1971; Zhang et al., 2014; Estornell et al., 2016), after ethylene treatment of leaf petioles when the pulvinus is shed (McManus et al., 1998), and after the induction of pedicel detachment by decapitation of flower buds (Lee et al., 2008; Hvoslef-Eide et al., 2016). Although individual, non-coherent petals are detached by a primary AZ located at their junction to the receptacle, when they are joined to one another to form a corolla tube, as the case of *Nicotiana* spp. flowers, an adventitious AZ is formed at the corolla base near its attachment to the receptacle during corolla abscission (Wu et al., 2012).

The identification of genes involved in the differentiation of primary AZs has been made possible through to the study of mutations affecting the AZs of floral organs and seeds in Arabidopsis, the AZs of several organs in legume species, the flower pedicel AZ in tomato, and the grain AZ between the lemma and pedicel or rachis in rice, sorghum, barley and wheat.

Floral organ abscission is prevented in the Arabidopsis *hws-1* and *ath1-3* mutants, affecting the putative F-box protein named HAWAIIAN SKIRT and the BELL-type ARABIDOPSIS THALIANA HOMEOBOX GENE1 (González-Carranza et al., 2007b; Gómez-Mena and Sablowski, 2008), while in *as1-1* and *as1-20* mutants, affecting the MYB transcription factor (TF) *ASYMMETRIC LEAVES1*, sepals and petals are retained until siliques are fully elongated (Gubert et al., 2014). All these mutants showed defects in the setting of organ boundaries in the flower receptacle, suggesting that their proper placement is required for AZ development. *BLADE-ON-PETIOLE* (*BOP*)-like genes, which encode BTB/POZ domain and ankyrin repeat

containing NPR1-like proteins, regulate the development of floral organ AZs in Arabidopsis (McKim et al., 2008), and petal, leaf, leaflets and fruit AZs in a number of legume species such as *Medicago truncatula*, *Lotus japonicus*, and *Pisum sativum* (Couzigou et al., 2016). In addition to regulating the ontogeny of several primary AZs, a *BOP*-like gene from cultivated tobacco (*Nicotiana tabacum*) has been involved in the formation of an adventitious AZ, the corolla AZ (Wu et al., 2012). The activity of the *knotted1*-like homeobox (*KNOX*) gene *BREVIPEDICELLUS* (*BP*) is required for the development of the architecture of the Arabidopsis inflorescence and for the proper differentiation of the floral organ AZs in the flower receptacle (Wang et al., 2006). The differentiation of the seed AZ in Arabidopsis is regulated by the MADS-box TF *SEEDSTICK* (*STK*) and the bHLH TF *HECATE3* (*HEC3*) (Pinyopich et al., 2003; Ogawa et al., 2009). In tomato, *jointless* (*j*) and *jointless2* (*j2*) mutations completely suppress flower pedicel AZ differentiation, and the *lateral suppressor* (*ls*) and *blind* (*bl*) mutations partially impair its development (Butler, 1936; Rick, 1956; Roberts et al., 2002; Schmitz et al., 2002; Shalit et al., 2009; Nakano et al., 2012). The *j* and *j2* loci encode MADS-box TFs (Mao et al., 2000; Roldan et al., 2017) while the *ls* and *bl* loci encode for a family of GRAS and MYB TFs, respectively (Schumacher et al., 1999; Schmitz et al., 2002). Another MADS-box TF, *MACROCALYX* (*MC*), which was identified as a regulator of sepal size (Vrebalov et al., 2002), also regulated tomato pedicel AZ development by interacting with the MADS-box protein encoded by the *j* locus (Nakano et al., 2012). The tomato TFs *SlBOP2* and *TERMINATING FLOWER* (*TMF*) belonging to the ALOG (Arabidopsis LSH1 and Oryza G1) protein family, have recently been implicated in the leaf axil proximal-distal patterning and, therefore, in the differentiation of the leaf AZ (Izhaki et al., 2018). Finally, the *M. truncatula* Lateral Organ Boundary (LOB) domain protein Petiolule-Like Pulvinus (PLP), which is closely related to Arabidopsis ASL4/LOB (Zhou et al., 2012a), is involved in the development of leaflet and petiole AZs (Du et al., 2020).

Grain dispersal (seed shattering/brittle rachis) in cereals is dependent on the formation of an AZ in the joint between the lemma and the pedicel or rachis. The domestication of wild cereals had a particular impact on certain traits, including the disarticulation of the spike (Doebley et al., 2006). The study of natural variation in seed shattering among cereal cultivars has allowed the identification of a number of genes involved in that process. In rice, pedicel AZ formation is regulated by two *BELL1* (*BEL1*)-type homeodomain TFs, *qSH1* and its paralog *SH5* (Konishi et al., 2006; Yoon et al., 2014), which are closely related to Arabidopsis *PENNYWISE* (*PNY*; also known as *BELLRINGER*, *BLR*, or *REPLUMLESS*, *RPL*), involved in pod dehiscence (Arnaud et al., 2011). Other genes of rice involved in pedicel AZ formation are *SHATTERING ABORTION1* (*SHAT1*) and *SUPERNUMERARY BRACT* (*SNB*), encoding *AP2* family TFs, *SHATTERING1* (*OsSH1*), encoding a *YABBY* family TF, the MYB-like protein *SH4,* and a *CTD phosphatase-like protein1* (*OsCPL1*) (Li et al., 2006; Ji et al., 2010; Lin et al., 2012; Zhou et al., 2012b; Wu et al., 2017; Lv et al., 2018; Jiang et al., 2019). Two different shattering genes were identified in sorghum, *Sh1* and *SpWRKY,* belonging, respectively, to the YABBY and WRKY families TFs (Lin et al., 2012; Tang et al., 2013). And two different loci, *brittle-rachis 1* (*Btr1*) and *brittle-rachis 2* (*Btr2*), encoding an α/β-hydrolase superfamily protein and a hypothetical protein, respectively, have been involved in the regulation of brittle rachis (seed shattering) in barley (Pourkheirandish et al., 2015). Homologs of these two genes, *Btr1* and *Btr2*, are also active in two wild wheat relatives, *Aegilops longissima* and *Aegilops tauschii*, which also result in seed shattering phenotypes (Zeng et al., 2020a; Zeng et al., 2020b; Zeng et al., 2020c).

1.3.2.2. Acquisition of competence to respond to abscission-promoting cues

Before the onset of the cell separation program, AZ cells must remain firmly attached to one another to allow continuous growth of the AZ until it is fully developed and competent to perceive and respond to abscission-stimulating signals. If the abscission signal is not provided by the subtending organ, then the AZ continues growing to gain a thicker structure necessary to support the growing organ. However, the abscission process is immediately initiated in AZ cells when the signal is provided, and this response is modulated by both “classical” hormones and perhaps by hormone peptides (see Figure 1.2).

There is plenty of experimental evidence supporting the idea that the competence of AZ cells to respond to abscission signals results primarily from the coordinated regulation of auxin and ethylene (extensive review on this subject can be found in Taylor and Whitelaw, 2001; Meir et al., 2015; Tucker and Kim, 2015; Botton and Ruperti, 2019). If auxin levels in the AZ are maintained by the subtending organ through polar auxin transport or, alternatively, by direct application of auxin or by genetically manipulating auxin synthesis, then AZ cells do not respond to ethylene. A correlation between the rate or the incidence of abscission and the abundance of transcripts encoding auxin influx (AUX1 and LAX proteins) and auxin efflux carriers (PIN and PIN-like proteins) and auxin regulatory proteins (Aux/IAA and auxin response factors) has been reported in floral organ AZs of Arabidopsis and rose, and tomato flower AZs (Meir et al., 2006; Basu et al., 2013; Meir et al., 2015; Gao et al., 2016; Shi et al., 2017). The tomato gene *KNOTTED1-LIKE HOMEOBOX PROTEIN1* (*LcKD1*), which is expressed in both the petiole and pedicel AZs, is a regulator of the abscission process (Ma et al., 2015). Knockdown of *LcKD1* resulted in a notable delay in leaf and flower abscission, while the abscission of these organs was accelerated in the tomato mutant *Petrosilenum*, carrying a semi-dominant mutation in *LcKD1*. The effect on abscission of the reduction in the transcriptional level of *LcKD1* was associated with the upregulation of Aux/IAA and SAUR factors and the downregulation of auxin efflux carriers, IAA-amino acid hydrolases, and auxin response factors (Ma et al., 2015). Hormone signals arising from organ senescence and stressful environmental conditions usually activate AZ cell responses through changes in biosynthesis and/or ethylene signaling (Brown, 1997; Roberts et al., 2002). An Arabidopsis auxin response factor, ARF2, modulates organ senescence and floral organ abscission through the regulation of the expression of three ACC synthases, but independently to the ethylene and cytokinin response pathways (Ellis et al., 2005; Okushima et al., 2005). It is worth mentioning that three MADS-box transcription factors, AGL15 and its closed family member AGL18, and AGL42/FYF (Forever Young Flower), are negative regulators of floral organ abscission in Arabidopsis (Fernandez et al., 2000; Adamczyk et al., 2007; Chen et al., 2011) and might participate in the response of AZ cells to abscission signals. It has been reported that auxin positively regulates the expression of both AGL15 and AGL18 (Zhu and Perry, 2004; Zheng et al., 2009), while AGL42/FYF negatively regulates the expression of the Ethylene Response DNA-Binding Factors EDF1/TEM1, EDF2/TEM2, EDF3/ARF4, and EDF4/RAV1 in floral organ AZ cells (Chen et al., 2015). Two *Phalaenopsis* orchid homologs of Arabidopsis AGL42/FYF, PaFYF1 and PaFYF2, are also able to regulate petal senescence and abscission by suppressing the expression of EDF genes (Chen et al., 2020). In addition to suppressing EDF expression in floral organ AZs, AGL42/FYF also negatively regulates the expression of the hormone peptide INFLORESCENCE DEFICIENT IN ABSCISSION (IDA) (Chen et al., 2011). IDA is a peptide ligand that binds to its receptor-like kinases HAESA (HAE) and HAESA-LIKE2 (HSL2) to control floral organ abscission in

Arabidopsis (for a recent review, see Shi et al., 2019). The abscission signaling module comprising IDA and the LRR-RLKs HAE and HSL2 is presented below in detail in section 1.4. The Arabidopsis MADS-box gene AGAMOUS (AG), one of the four genes whose initials give name to the gene family, also regulates floral organ senescence and abscission, not through auxin or ethylene, but through jasmonate (JA) biosynthesis (Jibran et al., 2017). Interestingly, JA levels in the floral receptacle modulated the expression of the MADS-box gene AGL15. Therefore, AG appears to regulate senescence and abscission of floral organs through JA and AGL15, and perhaps also through the IDA-HAE/HSL2 signaling module.

In addition to hormones, an AZ-specific gene set containing key regulators of meristem-associated genes is apparently necessary to maintain cell-to-cell adhesion and the competence to respond to abscission signals (Nakano et al., 2012, 2013; Nakano and Ito, 2013). These AZ-specific genes that might regulate the activity of tomato pedicel AZ cells are *Lateral suppressor* (*Ls*), encoding a VHIID protein that has high homology with proteins associated with the signal transduction of gibberellins (Schumacher et al., 1999), *GOBLET* (*GOB*), encoding a NAC-domain TF similar to Arabidopsis *CUC2* (Berger et al., 2009), *Blind* (*Bl*), encoding a MYB TF homolog to Arabidopsis *REGULATOR OF AXILLARY MERISTEM* (*RAX*) (Schmitz et al., 2002), and WUSCHEL (LeWUS), encoding a tomato homolog of Arabidopsis WUSCHEL (Mayer et al., 1998). It is also worth mentioning that all these TFs are regulated by the AZ development genes *JOINTLESS*, *JOINTLESS2* and *MACROCALYX* (Nakano et al., 2012; Liu et al., 2014), suggesting that the acquisition of competence to respond to abscission signals is dependent on and closely linked to stage 1 of the abscission process. Homologs of *Ls*, *GOB*, and *Bl* have been identified in rice flower pedicel AZs indicating that this mechanism of competence acquisition may be conserved in monocots and dicots (Nakano and Ito, 2013). Another TFs involved in the maintenance of plant meristems and also in organ polarity and identity of separation layer cells have been associated to stage 2 of the abscission process (Kim et al., 2016, 2019). This new set of transcription factors potentially involved in soybean leaf abscission includes YABBY, AP2-like, homeobox, zinc finger, and Trihelix family members. In conclusion, plant meristems, like AZs, include a set of small, tightly packed cells that are arrested in an apparently unspecialized or undifferentiated state (van Nocker, 2009). Then, a number of TFs might regulate the maintenance of both sets of static and inactive cells before the onset of organ growth in the SAM and the abscission in AZs, as well as the differentiation of the separation line inside the AZs.

1.3.2.3. Activation of the abscission process within the abscission zone and organ detachment

Abscission is a cell separation process occurring in organ AZs by disassembly of cell walls and dissolution of the middle lamella. Therefore, specific members of cell wall remodeling enzymes and modifying proteins (CWR) gene families are highly represented in organ AZs during cell separation and organ detachment. Pectin-methylesterases (PMEs), pectin-acetylesterases (PAEs), β-galactosidases (βGALs), xyloglucan endotransglucosylases / hydrolases (XTHs), β-xylosidases (βXYLs), α-xylosidases (αXYL), and expansins (EXPs) participate in cell separation during organ abscission, but there are members of another gene families such as endo-1,4-β-glucanases (cellulases, CELs), polygalacturonases (PGs), and pectate lyases (PLs) that also have a prominent role in the process (for detailed reports on this subject see

Kim et al., 2006; Lashbrook and Cai, 2008; Meir et al., 2010; Sun and van Nocker, 2010; Gil-Amado and Gomez-Jimenez, 2013; Merelo et al., 2017; Tranbarger et al., 2017).

Endomembrane trafficking is thought to be central to initiate the separation process, the subsequent secretion of CWR proteins, or the endocytosis of cell wall materials. High-throughput approaches to search genes associated with endomembrane trafficking have been developed in melon (Corbacho et al., 2013) and olive (Gil-Amado and Gomez-Jimenez, 2013) fruit AZs, citrus leaf and fruit AZs (Agustí et al., 2012; Merelo et al., 2019), and also in tomato flower AZs (Sundaresan et al., 2020). These studies have revealed that the sequential induction of genes encoding CWR proteins was mainly associated with the regulation of genes encoding Rab-GTPases, small GTPases and SNAREs. So far, only two Arabidopsis proteins have been clearly implicated by genetic and molecular analysis in the intracellular trafficking process associated with organ abscission: an Arabidopsis mutant named *nev/agd5* (nevershed) was isolated and selected for retaining the floral organs indefinitely due to defects in the Golgi structure in floral organ AZs (Liljegren et al., 2009). Later, a new *nev* allele called *mtv/agd5-11* displaying similar floral organ abscission defects was isolated (Sauer et al., 2013). NEVERSHED/AGD5 (NEV) is an ADP-ribosylation factor-GTPase-activating protein (ARF-GAP) that is thought to regulate intracellular traffic by linking cargo recruitment with vesicle formation (Spang et al., 2010). NEV participates in a clathrin-dependent trafficking pathway from the trans-Golgi network to the prevacuolar compartment in AZ cells necessary for floral organ abscission to occur (Liljegren et al., 2009; Sauer et al., 2013). It has been hypothesized that the floral organ abscission defect of *nev* was due to errors in the activation of HAE/HSL2 signaling (Liljegren, 2012). However, the transcriptional alteration in *nev* was mainly associated with the response to biotic stimulus and cell death and the presence of transcript levels of various CWR genes involved in floral organ abscission such as *QRT2* and *ADPG2*, that are similar to those found in WT floral receptacles (Taylor and Walker, 2018). The *nev* mutant shows a disorganized and ectopic lignification of the floral receptacle (Lee et al., 2018) that might interfere with the process of disassembly of the cell walls and dissolution of the middle lamella that typically occurs during abscission. The EVERSHED (EVR)/SUPPRESSOR OF BIR1 (SOBIR1) receptor-like kinase functions in organ abscission (Leslie et al., 2010) and in plant defense responses to bacterial and fungal pathogens as well (Liebrand et al., 2013; Zhang et al., 2013). Defects in *nev* AZ cells were rescued by a mutation in EVR/SOBIR1, suggesting that they might regulate endomembrane trafficking during abscission. It has been proposed that EVR/SOBIR1 may repress cell separation by altering the localization of the HAE/HSL2 receptors (Gubert and Liljegren, 2014).

A number of TFs belonging to different gene families have been implicated in the regulation of the expression of CWR proteins during abscission. The first TFs identified were three TGA-type bZIP of the class I (*PvTGA1.1*) and class II types (*PvTGA2.1* and *PvTGA2.2*) that enhanced the expression of the bean abscission cellulase (*BAC*) by binding to the 5'-UTR region (Tucker et al., 2002). Members of the AP2/ERF family have been associated with organ abscission in melon (Corbacho et al., 2013), soybean (Kim et al., 2016), cassava (Liao et al., 2016) or rose (Gao et al., 2019), but only a tomato gene, *SlERF52*, has been shown to regulate the expression of CWR genes in flower AZs (Nakano et al., 2014). *SlERF52* positively regulated the expression of three PGs (*TAPG1*, *TAPG2*, and *TAPG4*) and one CEL (*Cel5*) previously involved in flower petiole abscission (Meir et al., 2010; Nakano et al., 2013; Wang et al., 2013). In litchi, the HD-Zip subfamily I TF *LcHB2,* specifically upregulated by ethylene in flower AZs

(Li et al., 2015), bound the promoter sequences of two CELs, *LcCEL2* and *LcCEL8*, positively regulating their expression during abscission (Li et al., 2019). Two Arabidopsis TFs specifically expressed in AZs, the TFIIIA-type zinc finger protein *AtZFP2* and the DNA binding with one finger (DOF) factor *AtDOF4.7*, are negative regulators of abscission (Cai and Lashbrook, 2008; Wei et al., 2010). DOF proteins can physically interact with similar or different types of transcription factors forming heterodimers, and thus may regulate the expression of downstream targets. In fact, AtDOF4.7 and AtZFP2 interacted in yeast two-hybrid and bimolecular fluorescence complementation (BiFC) assays, suggesting that they might form an abscission-regulatory transcription complex *in planta* (Wei et al., 2010). Transgenic Arabidopsis plants overexpressing *AtDOF4.7* showed no abscission of floral organs, however, they were sensitive to ethylene, displaying the standard triple response and accelerating the senescence of floral organs, although the abscission deficiency was not rescued (Wei et al., 2010). Transcript levels of *IDA*, *HAE* and *AGL15* showed no significant changes in siliques of *AtDOF4.7* overexpressed plants compared with WT siliques, while two PGs (*ADPG2* and *At4g23820*) and three XTHs (*AtXTH7*, *AtXTH12*, and *AtXTH28*), previously involved in abscission (Lashbrook and Cai, 2008), were downregulated (Wei et al., 2010). Thus, prevention of floral organ abscission by *AtDOF4.*7, and maybe by *AtZFP2,* might be mediated by its negative regulatory role on the expression of CWR proteins. The timing of *AtDOF4.7* expression was accelerated in transgenic plants expressing Promoter$_{AtDOF4.7}$::GUS treated with ethylene but was deferred in crosses with ethylene-insensitive mutants such as *etr1-1* and *ein2-1*, suggesting that *AtDOF4.*7 expression might be regulated by ethylene (Wang et al., 2016). Moving to another level of interaction, the timing of Promoter$_{AtDOF4.7}$::GUS expression in transgenic plants in an *ida2* mutant background did not change in comparison with that in a WT background, but the expression level of *AtDOF4.7* was higher than in WT siliques (Wang et al., 2016). Furthermore, the floral organ abscission phenotype in crosses of *AtDOF4.7* overexpressing lines with *35S:IDA* did not show earlier abscission. Additionally, activation of MKK5 resulted in both a reduction in the amount of AtDOF4.7 and the partial rescue of the abscission deficiency in *AtDOF4.7* overexpressing plants. MPK3 and MPK6, the targets of MKK5, physically interacted with and were capable of phosphorylating AtDOF4 (Wang et al., 2016). Therefore, *IDA* and *AtDOF4.7* might operate in a common abscission regulatory pathway being a direct target of MPKs, which would place *IDA* upstream of *AtDOF4.7* in the pathway.

Components of the Arabidopsis cell wall remodeling machinery involved in organ abscission appear to be controlled by the signaling module formed by the IDA signaling peptide and its specific receptors HAESA (HAE) and HAE-like 2 (HSL2) (detailed information on this signaling module is provided below in section 1.4). Transcriptional profiling using microarrays and high throughput next-generation sequencing was used to study differential gene expression between WT and *ida-2* and *hae hsl2* flower receptacles (Liu et al., 2013; Niederhuth et al., 2013b). Most of the genes over-represented in both Arabidopsis mutants encoded cell wall components and proteins involved in cell wall organization and modification, such as PMEs, PGs, CELs, XTHs and EXPs, suggesting that the signaling module IDA-HAE/HSL2 regulated cell wall disassembly and modification. The emergence of lateral roots from the main root, another cell separation process, requires the activity of CWR proteins as well. Two root-specific soybean genes encoding IDA-like proteins, *GmIDL2a* and *GmIDL4a*, regulated the expression of at least four PGs, five XTHs, and four EXPs during lateral root emergence (Liu et al., 2018). These experimental results support the role of the IDA-HAE/HSL2 signaling module in the

regulation of CWR gene expression. However, based on numerous CWR genes apparently involved in abscission of soybean leaves (Kim et al., 2015), tomato (Meir et al., 2010; Kim et al., 2015) or yellow lupin flowers (Glazinska et al., 2017), and apple (Zhu et al., 2011), melon (Corbacho et al., 2013), olive (Gil-Amado and Gomez-Jimenez, 2013), litchi (Li et al., 2015) or citrus fruits (Xie et al., 2018), and the small number of regulated CWR genes described in receptacles of the *ida2* mutant and the *hae hsl2* double mutant of Arabidopsis (Liu et al., 2013; Niederhuth et al., 2013b), it has been speculated that the signaling module only regulates the expression of a subset of CWR genes involved in abscission (Meir et al., 2019). CWR gene families certainly comprise a high number of members, although given the large number of physiological processes in which they participate, it might also be assumed that only a subset of each of them would be related to the achievement of a particular physiological process. In any case, this possibility should be evaluated experimentally. The putative network of TFs regulated by the IDA-HAE/HSL2 signaling module and their target genes should be identified as well.

1.3.2.4. Differentiation of a protective layer

The last stage of abscission involves the differentiation of a periderm or protective layer on the surface of the separating tissue remaining in the plant body, creating a scar sealing the wounded tissue (Sexton and Roberts, 1982). The differentiation of a protective layer serves two main purposes: reducing the loss of water through the wounded surface of the separation layer and protecting the plant from pathogen attack and invasion. It has been widely reported that waxes, suberin or lignin are deposited in the protective layer and that, in addition, pathogenesis-related (PR) proteins accumulated in AZ cells and in its vicinity (for recent reviews, see Niederhuth et al., 2013a and Tucker and Kim, 2015).

Early studies on organ abscission showed evidence to support that the synthesis of the protective layer started as early as at stage 3 of abscission, both during cell separation and after organ detachment had commenced (Addicott, 1982). It has been reported that cell separation and defense responses appeared to be coordinated and simultaneous processes during ethylene-promoted citrus leaf abscission (Agustí et al., 2009). CWR proteins were preferentially expressed in laminar AZ (LAZ) cells located at the interface between the petiole and the leaf blade, and PR proteins in petiolar cortical cells located in the vicinity of the LAZ. In herbaceous plants such as Arabidopsis, soybean and tomato, the protective layer develops on or around the separation layer (Addicott, 1982; Meir et al., 2011; Kim et al., 2015), whereas in woody plants cell division was often observed on the proximal side of the AZ before the onset of abscission (as an example, see Merelo et al., 2017). The synthesis and deposition of a protective layer does not occur on the distal side of the AZ because that protection is not necessary for the detached organ.

The role of lignin deposition has been related with plant defense but it has been suggested that lignification might also facilitate the mechanical cell wall breakage during cell separation processes (Sexton, 1979; Liljegren et al., 2000). Lignin deposition was observed specifically on the distal side of citrus fruit AZs after 24 and 48 h of ethylene treatment and was associated with upregulation of phenylpropanoid biosynthesis and monolignol biosynthesis and deposition (Merelo et al., 2017). The localization of lignin deposition only on the distal side of the citrus fruit AZ strongly suggested that this polymer potentially acted by generating a tension in the

fracture plane to facilitate cell wall breakage during citrus fruit abscission, rather than forming protective layers (Merelo et al., 2017). Recently, lignin deposition in AZs has been closely related to the cell separation process (Yoon et al., 2017; Lee et al., 2018). In cereal crops such as rice, the flower AZ is differentiated at the junction between the lemma and the pedicel so that the caryopsis is detached with the lemma, while a short pedicel remains attached to the panicle (Dong and Wang, 2015). In non-shattering rice varieties, the pedicel area containing the AZ is heavily lignified while the AZ is lignin-free in varieties that easily disperse seeds, suggesting that lignin deposition protects cells from CWR protein activity (Yoon et al., 2017). Two cellular areas containing the so-called secession cells (SECs) and residuum cells (RECs) are distinguished in Arabidopsis floral organ AZs (Lee et al., 2018). The corners of several layers of SECs are lignified, resulting in a lignin-reinforced hexagonal structure that seems to act as a mechanical brace restricting the area where the CWR proteins will act, while a protective layer rich in waxes and cutin is deposited on the surface of the RECs (Lee et al., 2018). This last observation is in contrast to descriptions suggesting that a periderm-like protective layer containing mainly suberin is deposited on the surface of separation cell layers (Roberts et al., 2000; Hepworth and Pautot, 2015; Kim et al., 2015).

It has been hypothesized that in addition to cell separation associated with CWR protein activity, the biosynthesis and secretion of small 15-25 kDa proteins and cuticular waxes that began in abscission stage 3, form an extensible extracellular matrix and boundary layer on the surface of the soybean petiole, tomato pedicel and Arabidopsis floral organ separation layer that potentially enhanced organ detachment (Kim et al., 2015). The biosynthesis and deposition of this extensible extracellular matrix would also expand during abscission stage 4, together with the synthesis of a more rigid protective layer. The extracellular matrix is thought to contain PR proteins such as β-1,3-glucanases, chitinases, kunitz trypsin inhibitor and thaumatin. The identification of defense-related proteins associated with abscission have also been reported in floral organs, flowers, fruits, and leaves AZs of several plant species including Arabidopsis, bean, citrus, elderberry, peach, rose, and tomato (del Campillo and Lewis, 1992; Eyal et al., 1993; Coupe et al., 1995, 1997; Harris et al., 1997; Ruperti et al., 1999, 2002; Agustí et al., 2009; Meir et al., 2011; Höwing et al., 2014; Cheng et al., 2015; Singh et al., 2020).

The shedding of diseased organs is a general response of plants to pathogen infection. In Arabidopsis, cauline leaves infected with the bacteria *Pseudomonas syringae* are detached using the signaling module IDA-HAE/HSL2, operative during floral organ abscission (Patharkar et al., 2017). In addition, this pathogen-induced cell separation process is believed to be regulated by the phytohormone salicylic acid. An innate immune system is used by plants to protect themselves against diseases and mutants with impaired bacterial defense, such as *sid2*, *eds1-2*, *pad4-1*, and *NahG*, which are unable to shed their floral organs at the same rate as WT plants (Patharkar et al., 2017). A very recent report by Olsson and co-workers (2019) proposes that, in addition to inducing the expression of defense associated genes in floral organ AZs, the signaling peptide IDA together with PAMP-INDUCED PEPTIDE1 (PIP1) would promote heteromerization of HSL2 with RECEPTOR-LIKE KINASE 7 (RLK7), leading to the upregulation of defense genes in floral organ AZs. Parallel to the upregulation of CWR proteins by IDA and HAE/HSL2, PIP1 would activate RLK7 and FLAGELIN-SENSITIVE 2 (FLS2) receptors to upregulate both defense genes and IDA and this, in turn, would enhance HSL2 and RLK7 signaling. The similarity between PIP and PIP-like peptides and IDA and IDA-like peptides (Vie et al., 2015) would support this concerted action in the regulation of the defense

response and cell wall remodeling previously proposed during stress induced abscission (Wang et al., 2017). Thus, components of the abscission signaling module such as the IDA peptide and the LRR-RLK HSL2 may be involved in the modulation of the defensive response taking place in AZs.

A T2/S-like ribonuclease gene, *LX*, which is upregulated in tomato senescent leaves and by programmed cell death (PCD), has also been associated with organ abscission (Lers et al., 2006). In fact, transgenic downregulation of *LX* resulted in delaying tomato cotyledon and leaf abscission (Lers et al., 2006), suggesting that PCD might be required for organ abscission to occur. Another nuclease gene, *BFN1*, also associated with senescence and PCD, was specifically expressed in tomato leaf and fruit AZs and in Arabidopsis floral organ AZs (Farage-Barhom et al., 2008). In addition to the upregulation of *LX* ribonuclease, the expression of other PCD-associated genes, such as the nuclease *TBN1*, and cysteine and serine proteases, were also upregulated in the distal side of tomato leaf AZ together with β-1,3-glucanases and ACC synthases (Bar-Dror et al., 2011). Protease-encoding genes and other PCD-associated genes such as the metacaspase *AtMCP1b* and *RbPCD1* have been induced in rose, tomato, citrus and Arabidopsis AZs (Castillo-Olamendi et al., 2007; Helm et al., 2008; Tripathi et al., 2009; Kasaras and Kunze, 2010; Zhang et al., 2014; Singh et al., 2019). Therefore, PCD also occurs during the last stage of the abscission process and appears to be linked to the senescence process observed on the distal side of AZs.

1.4. The Arabidopsis abscission regulatory module INFLORESCENCE DEFICIENT IN ABSCISSION / HAESA-like receptor kinases

The experimental observation showing that floral organ abscission was not prevented but only delayed in ethylene-insensitive mutants of Arabidopsis such as *etr1-1* and *ein2-1*, led to the idea that, although ethylene accelerated the process, its perception was not essential to occur (Bleecker and Patterson, 1997). Therefore, ethylene-dependent and ethylene-independent abscission pathways might contribute to organ abscission in Arabidopsis. This idea was reinforced when several particular mutants of Arabidopsis showing significant delay in the timing of abscission were identified (Patterson and Bleecker, 2004). The *dab* (*delayed abscission*) mutants show the typical ethylene triple response, as well as accelerated leaf senescence and abscission of floral organs. The discovery of three ethylene-sensitive mutants led to the suggestion that an abscission signaling module including those components might operate in Arabidopsis: *ida* (*inflorescence deficient in abscission*) is a mutant lacking a peptide ligand that retained its floral organs indefinitely (Butenko et al., 2003, 2006), while repressing the leucine-rich repeat (LRR) receptor-like (RLK) kinase HAESA (Jinn et al., 2000) and overexpressing the MADS-box factor AGL15 (Fernandez et al., 2000), delayed floral organ abscission.

HAESA (HAE) and its paralog HAESA-LIKE2 (HSL2) were the first LRR-RLKs identified as essential for floral organ abscission in Arabidopsis (Jinn et al., 2000; Cho et al., 2008; Stenvik et al., 2008). They are transmembrane receptors, with an extracellular leucine-rich repeats (LRR) receptor ectodomain and cytoplasmic Ser/Thr protein kinase domains, that redundantly control abscission through the binding of a peptide ligand. The *IDA* gene was identified in

Arabidopsis mutants showing no abscission of floral organs (Butenko et al., 2003). It encodes a small (77 amino acids) prepropeptide containing an N-terminal signal sequence that directs it to the secretory pathway (Butenko et al., 2003). The IDA prepropeptide must follow an obligatory maturation pathway to become an active cell signaling element (Stührwohldt et al., 2017; Olsson et al., 2019b). The first maturation step is associated with its export to the endoplasmic reticulum where the N-terminal sorting sequence is cleaved off by a signal peptidase, resulting in an IDA propeptide. The following maturation step is the hydroxylation of Pro64 of the prepropeptide amino acid sequence by a prolyl-4 hydroxylase while the propeptide is still in the ER or already in the Golgi. Proline hydroxylation is required for maximum activity of the mature peptide and for receptor binding and activation (Butenko et al., 2014; Santiago et al., 2016). And finally, subtilases (a subfamily of serine proteases) SBT4.12, SBT4.13 and SBT5.2 proteolytically process the propeptide into a bioactive 14-mer IDA mature peptide (GVPIPPSA**P**SKRHN; Schardon et al., 2016). This last proteolytic activity is required for organ abscission to occur since transgenic Arabidopsis plants expressing the extracellular proteinase inhibitors EPI1a and EPI10 from the fungus *Phytophthora infestans* under the control of the IDA promoter retain their floral organs (Stührwohldt et al., 2018). So far, the actual active peptide of Arabidopsis has not been isolated *in planta* (Shi et al., 2019). However, a 14-mer EPIP peptide has recently been identified in anthers of tomato flowers by liquid chromatography-tandem mass spectrometry, whose application to flowers of knockout lines for *SlIDA1*, a tomato *AtIDA* homolog previously identified in flower AZs (Tucker and Yang, 2012), rescued the anther dehiscence deficiency (Wang et al., 2020).

The abscission analysis of *ida* mutant and *hae hsl2* double mutant revealed that both fail to shed floral organs (Butenko et al., 2003; Cho et al., 2008; Stenvik et al., 2008). The genetic analysis showed that the HAE/HSL2 receptor complex was epistatic to IDA. This, together with the nature of IDA as a small secreted peptide, suggested that it might be a ligand of the HAE and HSL2 receptor kinases, and prompted further studies to characterize an IDA/HAESA-like signaling pathway (Cho et al., 2008; Stenvik et al., 2008). When constitutively expressed in the wild-type background, *IDA* accelerated floral organ abscission and AZs were substantially larger than in wild-type flowers, and secreted an arabinogalactan-enriched substance (Stenvik et al., 2006; Shi et al., 2011). In addition, ectopic abscission occurred at the base of pedicels, branches and cauline leaves, where vestigial AZs are found (Stenvik et al., 2006). The abscission phenotype was not rescued when *IDA* was ectopically overexpressed in *hae hsl2* double mutant background (Stenvik et al., 2006). Thus, functional HAESA-like receptors are required by IDA to trigger organ abscission. Biochemical studies demonstrated a direct correlation between IDA activity and HAE/HSL2 receptor affinity (Butenko et al., 2014). Floral organ abscission does not occur in ethylene-treated *ida* mutant plants, although they show typical ethylene responses (Butenko et al., 2003, 2006), an observation related to the fact that *HAE* expression was independent of ethylene signal transduction (Jinn et al., 2000). Taken together, these experimental observations suggested that the IDA-HAE/HSL2 signaling module participates in an ethylene-independent abscission pathway. However, ethylene induces both *IDA* and *HAE* gene expression, which raises some questions about whether or not the activity of IDA-HAE/HSL2 participates in the ethylene-independent abscission pathway. Ethylene treatment of soybean and tomato leaves and citrus fruits induced the expression of *IDA*-like genes in AZs (Tucker and Yang, 2012; Estornell et al., 2015), and treatment with the ethylene action inhibitor 2,5-norbornadiene blocked leaf abscission and reduced *IDA*-like gene expression in soybean (Tucker and Yang, 2012). In addition, ethylene also induced *IDA*-like

gene expression in yellow lupin flower AZs (Wilmowicz et al., 2018), and the expression of *HAE*-like gene was also induced in oil palm (Stø et al., 2015) and litchi fruit AZs (Ying et al., 2016; Wang et al., 2019a). All these experimental observations point to the possibility that the IDA-HAE/HSL2 signaling module might control the abscission process downstream of ethylene (Meir et al., 2019).

One of the most common mechanisms for activating downstream intracellular modules in RLK signaling is the ligand induced receptor heterodimerization (Li et al., 2002; He et al., 2013). SOMATIC EMBRYOGENESIS RECEPTOR KINASE (SERK) is a family of LRR-RLKs consisting of five members in Arabidopsis, SERK1-5, although SERK5 is likely a non-functional kinase (Gou et al., 2012). Family members SERK1-4 participate in brassinosteroids perception (Li et al., 2002; Nam and Li, 2002; Gou et al., 2012), bacterial defense (Chinchilla et al., 2007; Heese et al., 2007; Roux et al., 2011), as well as in other growth and developmental processes (Liebrand et al., 2014; Aan den Toorn et al., 2015; Ladwig et al., 2015; Meng et al., 2015; Wang et al., 2015). It was reported that all four functional SERK family members, SERK1-4, redundantly regulate floral organ abscission (Meng et al., 2016). Upon IDA binding and establishment of the complex with HAE/HSL2, a SERK RLK is recruited as a co-receptor that directly heterodimerizes with HAE and HSL2. Epistasis studies revealed that SERKs function genetically downstream of IDA and upstream of a mitogen-activated protein kinase (MAPK) cascade. In addition, HAE and SERK3 transphosphorylate each other in vitro. Structural studies also supported the formation of a stable HAE/SERK1 heterodimer upon IDA reception (Santiago et al., 2016). Therefore, the IDA-stabilized, HAE/HSL2-SERK complex transphosphorylates and relays the signal to a MAPK cascade to control floral organ abscission (Liljegren, 2012; Niederhuth et al., 2013a; Meng et al., 2016; Santiago et al., 2016).

Mitogen-activated protein kinase kinase 4 (MKK4) and MKK5 and mitogen activated protein kinase 3 (MPK3) and MPK6 act together in different signaling cascades for a variety of processes, including embryogenesis, innate immunity or stomatal development and patterning (Wang et al., 2007; Zhao et al., 2014; Zhang et al., 2017). Genetic studies revealed that *mkk4 mkk5* and *mpk3 mpk6* double mutants fail to abscise their floral organs, while their constitutive expression restores abscission in a *hae hsl2* double mutant background (Cho et al., 2008). Therefore, this MAPK cascade is epistatic to the HAE/HSL2 receptor complex, thus becoming the downstream member of the signaling module by relaying the phosphorylation signal (Cho et al., 2008; Patharkar and Walker, 2018). Positioned on another level within the abscission signaling module is the MADS-box factor AGL15. Overexpression of AGL15 delayed abscission, suggesting that it operates as a negative regulator of the process (Fernandez et al., 2000), and also results in decreased expression of *HAE* by binding to its promoter sequence (Patharkar and Walker, 2015). The MAPK cascade involving MKK4/MKK5 and MPK4/MPK6 phosphorylates AGL15 once the abscission signaling pathway is activated, releasing then the repression of *HAE* expression. Therefore, it appears that a positive signal loop connecting components downstream the MAPK cascade with the expression of *HAE* positioned upstream would allow to amplify the abscission starting signal (Patharkar and Walker, 2015).

Screening for mutations that restored floral abscission in *ida* mutants led to identification of the KNOTTED-LIKE HOMEOBOX transcription factor BREVIPEDICELLUS (BP) / KNOTTED-LIKE FROM ARABIDOPSIS THALIANA1 (KNAT1) (Butenko et al., 2012). BP/KNAT1 is involved in different processes including xylem fiber differentiation, root-skewing responses and

inflorescence architecture (Douglas et al., 2002; Qi and Zheng, 2013; Felipo-Benavent et al., 2018). *knat1* mutants resembled *IDA* overexpressing phenotype (accelerated abscission of floral organs and enlarged AZs), indicating a potential role as a negative regulator of abscission operating downstream of IDA signaling (Shi et al., 2011). It was determined that the MKK4/5 MPK3/6 MAPK cascade inhibits the activity of KNAT1, which in turn de-represses KNAT2 and KNAT6 to induce the expression of CWR proteins that allow cell separation (Shi et al., 2011; Butenko et al., 2012). Taken altogether, the aforementioned findings lead to the current molecular model of the IDA/RLKs abscission signaling module (Figure 1.3).

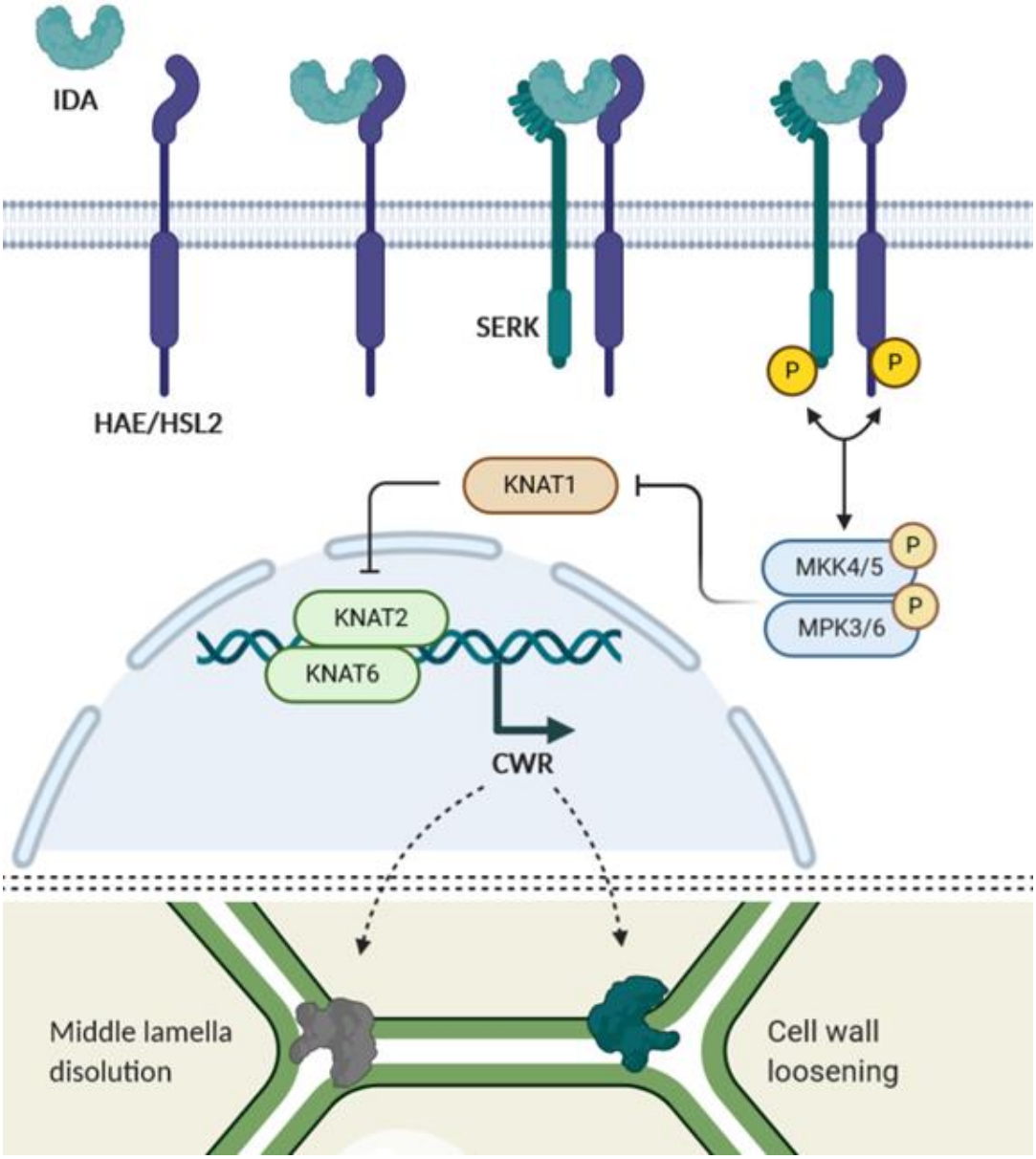

Figure 1.3. A proposed model for the IDA-HAE/HSL2 abscission signaling pathway. The binding of IDA to HAE/HSL2 receptors induces their heterodimerization to co-receptors of the SERK family, and leads to transphosphorylation of tyrosines in the cytoplasmic kinase domains and activation of the receptor complex. The signal from the receptor complex is transduced through a MAPK cascade consisting of MKK4/MKK5 and MPK3/MPK6. The signal transduced by the MAPK cascade then releases the transcriptional activity of KNAT2/6 avoided by BP/KNAT1, resulting in the upregulation of a set of cell wall remodeling enzymes and modifying proteins (CWR). These CWR proteins participate in the loosening of cell walls and the dissolution of the AZ middle lamella leading to organ detachment (Adapted from Butenko et al., 2012; Meng et al., 2016).

The *IDA* gene identified by Butenko and co-workers (2003) belongs to a gene family with eight additional *IDA*-like (*IDL*) members in Arabidopsis: *IDL1-8* (Vie et al., 2015). They all share a structure consisting of a signal peptide in the N-terminal portion of the prepropeptide, a variable region, and a conserved C-terminal PIP domain that is thought to confer bioactivity to mature peptides (Stenvik et al., 2008; Vie et al., 2015). *IDL1-5* genes have been postulated to function during plant development (Butenko et al., 2003; Stenvik et al., 2008). They follow different expression patterns with respect to *IDA*, but their overexpression resemble the phenotype of *35S:IDA*, suggesting that they could signal through the same IDA receptors (Stenvik et al., 2008). The spatial and temporal GUS activity of genes *IDL2-5* suggests its involvement in processes related to the development of the vascular system and also to the stomatal function (Stenvik et al., 2008). Although these genes retain some cell separation activity in the floral organs AZs, only *IDL1* can rescue the *ida* abscission deficiency when expressed under the *IDA* promoter (Stenvik et al., 2008). IDL7 and possibly IDL6 negatively modulate stress-induced reactive oxygen species (ROS) signaling in Arabidopsis (Vie et al., 2017), suggesting a broader spectrum of processes controlled by peptide hormone signaling. IDL6-8 seem to play a role in late stages of seed development or senescence (Vie et al., 2015).

In addition to controlling the signaling of aerial organ shedding, the IDA-HAE/HSL2 signaling module also participates in cell separation processes taking place in the root. Lateral roots are important for root architecture and determine the anchorage of plants in soil as well as the uptake of water and nutrients. Lateral root development is a multistep developmental process consisting of four different phases: positioning, initiation, morphogenesis and emergence (He and Meng, 2020). IDA and IDL1, by interacting with HAE and HSL2, participate in cell separation of the root endodermis, cortex, and epidermis from the main root until the lateral roots emerge (Kumpf et al., 2013). Consistently, mutations in *IDA*, *HAE* of *HSL2* delay lateral root emergence (Kumpf et al., 2013). Upon interaction between IDA and HAE/HSL2, the signal is transduced through MKK4/MKK5 and MPK3/MPK6, the same MAPK cascade that participates in the IDA pathway for floral organs abscission (Zhu et al., 2019). Interestingly, this MAPK cascade participates in the morphogenesis step of lateral root formation but under the control of auxins (Huang et al., 2019). In addition to the emergence of lateral roots, the IDA-HAE/HSL2 signaling module also controls root cap sloughing. The root cap protects the stem cell niche of angiosperm roots from damage associated with soil penetration (Arnaud et al., 2010). The size of the root cap is constant and is determined by a homeostatic balance between generation and loss of root cap cells (Kumpf and Nowack, 2015). IDL1 regulates this homeostatic balance between stem cell division and sloughing activity at the root cap in Arabidopsis through its binding to HSL2 (Shi et al., 2018).

Considering the above information, it seems obvious that abscission in Arabidopsis is controlled by the signaling module IDA-HAE/HSL2. It has been reported in crop species such as tomato, soybean, citrus, litchi, oil palm, and yellow lupine, that specific members of the *IDA*-like gene family were highly expressed in leaf, flower and fruit AZs (Tucker and Yang, 2012; Estornell et al., 2015; Stø et al., 2015; Ying et al., 2016; Wilmowicz et al., 2018), suggesting that they might conserve functions similar to that of *AtIDA* in regulating cell separation during organ abscission. It has also been shown that synthetic IDA peptides were able to induce early floral organ abscission in Arabidopsis (Stenvik et al., 2008), and to promote flower, mature fruit, and leaf abscission in yellow lupine, oil palm and Poplar, respectively (Wilmowicz et al., 2018; Tranbarger et al., 2019). Additionally, *IDA* homologs of citrus (*CitIDA3*) and litchi (*LcIDA1*) were

functional when heterologously expressed in Arabidopsis producing earlier floral organ abscission and rescuing the *ida2* abscission deficiency (Estornell et al., 2015; Ying et al., 2016). Similarly, the ectopic overexpression of a *HAE*-like homolog of litchi, *LcHSL2*, was able to completely rescue the abscission phenotype in the Arabidopsis double mutant *hae/hsl2* (Wang et al., 2019a). Finally, the ectopic expression of *LcKNAT1*, the litchi homolog of Arabidopsis *BP/KNAT1*, prevented the abscission of flowers and floral organs in tomato and Arabidopsis, respectively (Zhao et al., 2020). This abscission response regulated by LcKNAT1 was mediated by its binding to ACC synthase and ACC oxidase promoters, repressing gene expression and thus ethylene biosynthesis. Despite the high number of results pointing to the conservation of this signaling module in various angiosperms, there is still some reluctance in the scientific community to generalize the function of this module to other plant species (Meir et al., 2019). Therefore, it would be advisable to provide unequivocal demonstration of its functionality in plant species other than Arabidopsis, to address the doubts and objections that still remain regarding the conservation of the IDA-HAE/HSL2 abscission signaling module.

2
Aims and design of the present study

The regulatory function of the signaling module IDA-HAE/HSL2 in different cell separation processes such as abscission of floral organs (Butenko et al., 2003, 2012; Stenvik et al., 2006, 2008), emergence of lateral roots (Kumpf et al., 2013) and root cap sloughing (Shi et al., 2018) has been reliably demonstrated in the model plant *Arabidopsis thaliana* (Arabidopsis). In addition to Arabidopsis, *IDA*-like genes have also been identified in a number of crop species, although a regulatory function in the emergence of lateral roots has only been demonstrated in soybean (Liu et al., 2018).

It has been reported that specific members of the *IDA*-like gene family in tomato, soybean, citrus, litchi, yellow lupine, and oil palm are highly expressed in leaf and fruit abscission zones (Tucker and Yang, 2012; Estornell et al., 2015; Stø et al., 2015; Ying et al., 2016; Wilmowicz et al., 2018), therefore suggesting that they may have conserved functions similar to *AtIDA* in regulating cell separation during organ abscission. It has also been shown that synthetic IDA peptides are able to induce early floral abscission in Arabidopsis flowers (Stenvik et al., 2008), and to promote flower, mature fruit and leaf abscission in yellow lupine, oil palm and Poplar, respectively (Wilmowicz et al., 2018; Tranbarger et al., 2019). Additionally, *IDA* homologs of citrus (*CitIDA3*) and litchi (*LcIDA1*) are functional when heterologously expressed in Arabidopsis, producing earlier floral organ abscission and rescuing the *ida2* abscission deficiency (Estornell et al., 2015; Ying et al., 2016). Similarly, the ectopic over-expression of a *HAE*-like homolog of litchi, *LcHSL2*, is able to completely rescue the abscission phenotype of floral organs in the Arabidopsis double mutant *hae/hsl2* (Wang et al., 2019a). While these results provide evidence to suggest conservation of function for *IDA* in a number of species, further unequivocal demonstration of the functionality of those IDA-like genes in organ abscission remains to be provided.

Therefore, based on the pioneering work in Arabidopsis by Butenko and co-workers (2003) and subsequent work by the Group of Dr. Reidunn B. Aalen and Dr. Melinka A. Butenko, and also encouraged by ensuing studies in agronomic and horticultural crops, the present study was conceived to identify and determine the extent of physiological functions related to abscission of the corolla tube of specific genes of the *IDA*-like and HAE-like families in the solanaceous *Nicotiana benthamiana.*

The research objectives were:

1. To identify genes belonging to the *IDA*-like and *HAE*-like families in several economically important species of the Solanaceae family, and discriminate those specific members in *Nicotiana benthamiana* that are involved in organ abscission and other developmental processes.

2. To examine the corolla abscission behavior of *N. benthaniana* flowers in response to VIGS-based silencing and/or overexpression of abscission-related *NbenIDA* and *NbenHAE* genes, in order to elucidate whether the IDA-HAE/HSL2 module regulating organ abscission in Arabidopsis is conserved in other angiosperms.

3
Materials and methods

Sequences retrieval and analysis

The EPIP motif of AtIDA (FGYLPKGVPIPPSAPSKRHNSFVNSLPH) was used to identify the *IDA*-like members of the selected Solanaceae species (*N. sylvestris, N. tomentosiformis, N. tabacum, N. benthamiana, Solanum lycopersicum, S. tuberosum, S. melongena and Capsicum annuum*) by tBLASTn and BLASTp inquiries in the Sol Genomics (Mueller et al., 2005) web platform (https://solgenomics.net/tools/blast/), depending on the databases status. “N.sylvestris Genome”, “N.tomentosiformis Genome”, “N.tabacum BX Genome”, “N.benthamiana v1.0.1”, “Tomato ITAG release 3.20”, “Potato PGSC DM v3 scaffolds”, “Eggplant draft genome (release 2.5.1)” and “Capsicum annuum UCD10X genome chromosomes (v1.0)” databases (Bombarely et al., 2012; Tomato Genome Consortium, 2012; Sierro et al., 2013; Sierro et al., 2014; Edwards et al., 2017; Hulse-Kemp et al., 2018) were used, respectively. Arabidopsis AtHAE, AtHSL1 and AtHSL2 protein sequences were retrieved from Phytozome v12.1 and TAIR10 databases and were used to identify the *HAE*-like members of the selected Solanaceae species in the same way as described above. Newly identified genes were named numerically, adding an “A”, “B”, “.1” or “.2” termination to the *IDA*-like or *HAE*-like gene pairs for the allotetraploids *N. tabacum* and *N. benthamiana*.

Sequence alignments were performed through MEGA7 software (Kumar et al., 2016) using the ClustalW algorithm with default parameters (DNA Data Bank of Japan, DDBJ; http://clustalw.ddbj.nig.ac.jp/). Phylogenetic trees were created using the Neighbor-Joining method (Saitou and Nei, 1987) using 1000 bootstrap replicates. The trees were drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic trees. The evolutionary distances were computed using the Poisson correction method (Troadec et al., 1998) and are presented in the units of the number of amino acid substitutions per site. All ambiguous positions were removed for each sequence pair (pairwise deletion option).

Prediction of peptide cellular localization site and the signal peptide in the IDA-like amino acid sequences was performed using the TargetP (Emanuelsson et al., 2000) and SignalP-5.0 (Almagro Armenteros et al., 2019) on-line tools. Up to 1000 base pairs of the 5′ untranslated region (5′ UTR) upstream from the initiation codon of the *IDA*-like genes of the *Nicotiana* species available in Sol Genomics databases were retrieved and submitted for *cis*-acting

regulatory element analysis in PlantCARE (Lescot, 2002). Schematic representations of regulatory elements of the promoter sequences were created using IBS1.0.3 software (Liu et al., 2015).

Plant materials and growth conditions

N. benthamiana seeds were germinated on nutrient soil and plantlets were transplanted individually in small pots with an artificial potting mix (50% vermiculite and 50% peat moss) in a plant growth chamber at 20/24 °C (night/day), 60% relative humidity and a 16/8-h light/dark regime. Water stress was induced by not watering the plants for 6 and 8 days for mild and severe stress conditions respectively.

RNA extraction

Basal portion of the corollas at different flower developmental stages as well as the rest of studied tissues were manually collected from the plants and frozen with liquid nitrogen. The tissue was grinded using Thomas Scientific's Liquid Nitrogen Cooled Mortar. Total RNA was extracted using Macherey-Nagel's NucleoSpin® RNA Plant, following the manufacturer's instructions. cDNA was synthesized from the RNA extraction using Thermo Fisher Scientific's SuperScript™ II Reverse Transcriptase, following the manufacturer's instructions.

qPCR analyses

Quantitative PCR analyses were performed using LightCycler® FastStart DNA MasterPLUS SYBR Green I reaction mix and a LightCycler 2.0 instrument (Roche, Basel, Switzerland) using gene-specific primers designed based on transcriptome sequences using the Primer3Plus software (Untergasser et al., 2012). Primer pairs are listed in Supplemental Data S1. Specificity of all the primer pairs used in this work was assessed by primer BLAST and melting curve analysis (Bustin and Huggett, 2017; Terol et al., 2019). The fluorescence intensity data was obtained through LightCycler Software version 4.1. The *N. benthamiana* housekeeping gene *NbenPP2A* (Liu et al., 2012) was used for normalization in all qPCR reactions carried out in this work. Three biological replicates were run for assessing the expression values of each gene. The averaged expression values were obtained in the form of Ct (cycle threshold) and all the analyses were performed through $2^{-\Delta\Delta CT}$ method.

IDA-like and *HAE*-like genes expression was normalized respect to that of *NbenPP2A* in different plant tissues and organs in wild type plants. In apical buds, nodes, internodes, corolla, style and stigma, and root tissues, gene expression values were relativized to the lowest expression value of each gene in the relevant tissue or organ, within primer sets. In leaf, anthers, fruits and corolla base tissues, gene expression values were relativized to the expression value of the earliest developmental stage relevant for that tissue (young leaf, anthers and fruits in stage 2, and corolla base of a stage 1 flower, respectively) within primer sets. Units were represented as the log2 of the fold change. In the case of leaf, anthers, fruits and base of the corolla tissues, red color indicates that the gene is upregulated (values over 0); white, that remain unchanged (values close to 0); and blue, that the gene is downregulated

(values under 0); all respect to *NbenPP2A* expression in the corresponding tissue in its earliest developmental stage.

In the water stress experiment, *NbenPP2A* was also used as a housekeeping gene for normalization, and watered tissue expression values as a relative reference, thus constituting our control conditions. Conditions were appropriate for each measurement, using the corresponding control tissue (leaf or root of watered plants) as a relative reference. Units were represented as fold change. Red color indicates that the gene is upregulated (values over 1); white, that remain unchanged (values close to 1); and blue, that the gene is downregulated (values under 1); all respect to *NbenPP2A* expression in the corresponding watered (control) tissue.

CLBV constructs

CLBV-based vectors developed by Agüero et al., 2012 were used to develop the genetic constructs utilized for silencing and overexpressing genes. Coding regions of *NbenIDA1A* and *NbenHAE.1* were amplified by RT-PCR from *N. benthamiana* RNA extracts using proper primers, and amplified fragments of said genes were inserted into the *PmlI* restriction site of the *clbv3'* vector (Agüero et al., 2012) to generate the *clbv3'*-NbenIDA and *clbv3'*-NbenHAE silencing constructs, respectively. The complete coding sequences of *NbenIDA1A*, *CitIDA3* and *AtIDA* were amplified by RT-PCR from *N. benthamiana*, citrus and Arabidopsis RNA extracts using proper primers and were inserted into the *PmlI* restriction site of the *clbv3'pr* vector (Agüero et al., 2012) to generate the *clbv3'pr*-NbenIDA1, *clbv3'pr*-CitIDA3 and *clbv3´pr*-AtIDA overexpressing constructs, respectively.

Inoculation

All the recombinant plasmid constructs were transfected to *Agrobacterium tumefaciens* strain COR 308, and agroinfiltrated on *N. benthamiana* leaves as described in Vives et al., 2008.

Corolla breakstrength measurements

The force (in gram-force; gf) required to pull the corolla off the flower receptacle was measured using a Pesola® spring dynamometer (spring scale, 100g, d=1.0g, green with clamp, Micro Line). The clamp of the dynamometer was carefully attached to the corolla of *N. benthamiana* flowers, and force was applied until the corolla detached from the flower receptacle. Every corolla detachment event was recorded using a video camera. The videos were examined frame-by-frame to determine the magnitude of the force applied to separate the corollas.

Corolla base anatomy

Flowers from *N. benthamiana* plants inoculated with the control *clbv3'* vector (wild-type plants) and *clbv3'*-NbenIDA construct were sampled at developmental stages 5 (onset of corolla senescence with margins of the corolla limb lobes curling inwards) and 6 (corolla limb completely contracted and brown and corolla tube drying).

Samples containing the capsule and the base of the corolla tube attached to the flower receptacle were fixed and embedded in LR White resin (London Resin Co., Woking, Surrey, UK) according to Tadeo et al. (1995). Longitudinal sections (about 1 µm thick) were cut with a Leica RM2255 microtome (Leica Microsystems, Wetzlar, Germany) using glass knives and fixed to microscope slides. Sections were stained with Toluidine Blue O (CI 52040; Merck, Darmstadt, Germany) after O'Brien et al. (1964) and examined and photographed with a Leica DM LA microscope (Leica Microsystems, Wetzlar, Germany).

Next generation sequencing (NGS)

Samples collection and RNA extraction

Total RNA from the base of corolla tubes in flowers from plants inoculated with the empty *clbv3'* vector and the silencing constructs *clbv3'*-NibenIDA and *clbv3'*-NibenHAE was isolated using acid phenol extraction and lithium chloride precipitation method as described in Ecker and Davis (1987). Quality of the isolated total RNA was checked and quantified using the Nanodrop.

Illumina TruSeq™ RNA sequencing library preparation

The isolated total RNA was used for library construction. Pair-end libraries were prepared using the TruSeq™ RNA sample preparation kit (Illumina Inc.,) according to the manufacturer's protocol. Briefly, 0.5 µg of total RNA was used for poly-A based mRNA enrichment selection using oligo-dT magnetic beads followed by fragmentation by divalent cations at elevated temperature resulting into fragments of 80-250 nt, with the major peak at 130 nt. First strand cDNA synthesis by random hexamers and reverse transcriptase was followed by the second strand cDNA synthesis performed using RNAseH and DNA Pol I. Double stranded cDNA was end repaired, 3'adenylated, and the 3′- "T" nucleotide at the Illumina adaptor was used for the adaptor ligation. The ligation product was amplified with 15 cycles of PCR.

Sequencing, base calling and quality trimming

Each pair-end library was sequenced using TruSeq SBS Kit v3-HS, in paired end mode with the read length 2x76bp. A minimum of 50 million paired end reads for each sample was generated on HiSeq2000 (Illumina, Inc) following the manufacturer's protocol. Images analysis, base calling and quality scoring of the run were processed using the manufacturer's software Real Time Analysis (RTA 1.13.48) and followed by generation of FASTQ sequence files by CASSAVA. FASTQ files were pre-processed with Trimmomatic 0.38 (Bolger et al., 2014), and reads with average quality smaller than 25 and shorter than 36 bases were filtered.

Mapping next generation sequencing reads to reference genome

The transcriptome and the genome sequences of *N. benthamiana* (Bombarely et al., 2012) were used as reference for sequence read mapping using the STAR RNA-seq aligner with default parameters (Dobin et al., 2013) as implemented in the OmicsBox suit (https://www.biobam.com/omicsbox).

4

Identification and molecular analysis of *INFLORESCENCE DEFICIENT IN ABSCISSION (IDA)*-like genes and *HAESA (HAE)*-like receptor kinases in Solanaceae species of agronomic importance

Solanaceae is a large plant family with approximately 90 genera comprising more than 3000 species found on almost all continents. Solanaceae is also one of the most economically important families worldwide. Some species of this family such as tomato (*Solanum lycopersicum*), potato (*S. tuberosum*), eggplant (aubergine; *S. melongena*) and pepper (*Capsicum annum*) are of great relevance as a human food source. Overall, more than 29 million hectares of these Solanaceae food species were cultivated globally in 2016, producing 644 million metric tons with a net production value of more than 146 billion US dollars (http://www.fao.org/faostat). Thus, in addition to being important in human nutrition, they are also relevant in economic and social terms. Other Solanaceae such as tobacco (*Nicotiana* spp.) have medical importance as a source of plant drugs, while *Nicotiana benthamiana* is considered a relevant model organism for the study of plant-microbe interactions and also in plant molecular research and biotechnology (Goodin et al., 2008; Bally et al., 2018). In this initial piece of work, the conservation and phylogeny of the *INFLORESCENCE DEFICIENT IN ABSCISSION* (*IDA*)-like and *HAESA* (*HAE*)-like gene families is first determined by taking advantage of the free availability of the diploid genome sequences of tomato, eggplant, pepper, *N. Sylvestris*, *N. tomentosiformis*, the allopolyploids *N. tabacum* and *N. benthamiana*, and the double haploid genome sequence of potato in the Solanaceae Genomic Network (SGN; https://solgenomics.net/). Allopolyploidy is a type of whole genome duplication derived from hybridization of two or more diverged taxa, that primarily occurs through the fusion of unreduced (2n) gametes. The result of this kind of genome merging is the occurrence of pairs of homolog genes from each of the diploid parents in the allopolyploid genome, called homeologs (Glover et al., 2016). Therefore, in the allopolyploid genomes of *N. tabacum* and *N.*

benthamiana there will probably be pairs of homeologs for many of the members of the gene families.

The expression of the homeolog genes of the *IDA*-like and *HAE*-like families in different developing tissues and organs of *N. benthamiana* was then examined. In this way, both the identification and the discrimination of those members of these gene families involved in development processes such as organ abscission, stem growth and response to drought conditions will be carried out. The abscission of the corolla, the only organ that undergoes abscission in *N. benthamiana*, should be highly similar to that reported in *N. tabacum* (Wu et al., 2012). Corolla abscission in cultivated tobacco flowers is due to the dissolution of the middle lamella and apparently to the breakdown of the parenchyma cells at the base of the corolla tube, a process that results in the detachment of the senescent corolla. Furthermore, the effect of water stress on several species of this contrasted family has been the subject of major research and the physiological responses of these plants are also well known (Tani et al., 2018; Wang et al., 2018; López-Serrano et al., 2019).

4.1. The *IDA*-like gene family in the Solanaceae

IDA-like genes were searched in relevant genera of the Solanaceae family including several species of *Nicotiana* (*N. sylvestris*, *N. tomentosiformis*, *N. tabacum* and *N. benthamiana*), and other crops of agronomic interest such as tomato (*Solanum lycopersicum*), potato (*S. tuberosum*), eggplant (*S. melongena*) and pepper (*Capsicum annuum*) (Table 4.1 and Supplemental Data S2). All prepropeptides presented in Table 4.1 are predicted to be localized in the secretory pathway according to TargetP (Emanuelsson et al., 2000) and SignalP-5.0 (Almagro Armenteros et al., 2019). This gene family was first identified in *Arabidopsis thaliana* (from now on, Arabidopsis) (Butenko et al., 2003) and later in a number of Angiosperms (Stø et al., 2015). Their members contained a signal peptide targeting the protein to the apoplast through the secretory pathway and a conserved C-terminal part, the PIP motif, 12 amino acids long. The presence of a signal peptide in the sequence of all identified genes suggested a mechanism of posttranslational maturation in the apoplast similar to that described in Arabidopsis. The prepropeptide is proteolytically processed from a conserved 20-amino acid proline-rich region called the extended PIP (EPIP) by subtilisin-like serine proteinases to yield a bioactive peptide 14 amino acids long (Schardon et al., 2016). This proteolytic activity is required for organ abscission to occur, since transgenic Arabidopsis plants expressing the extracellular proteinase inhibitors EPI1a and EPI10 from the fungus *Phytophthora infestans* under the control of the IDA promoter, retain their floral organs (Stührwohldt et al., 2018).

All prepropeptides identified in this search showed a signal peptide, a variable region and a highly conserved C-terminal PIP domain (Figure 4.1). *IDA*-like families of the *Nicotiana* species *N. sylvestris* and *N. tomentosiformis* consisted of 5 members, while in the allopolyploids *N. benthamiana* and *N. tabacum* these families are formed by 5 pairs of homeologs, with one exception corresponding to *NbenIDA4*, whose homeolog pair was not found in the genomic screening. *All IDA*-like genes found in *Nicotiana* are new identifications, as the six members found in *S. melongena* and *C. annuum* and the seven members of the *S. tuberosum* family. In *S. lycopersicum*, five out of the eight *IDA*-like genes detected, members 1 to 5, were already described (Tucker and Yang, 2012) and named *SlIDA1-5*, while the other three peptides, *SlycIDA6-8*, are incorporated in the current work.

Table 4.1. *IDA*-like gene families in agronomically important species of the Solanaceae family. [a] Sol Genomics Network (Fernandez-Pozo et al., 2015). The CINEMA color scheme is used to show the chemical nature of the amino acid residues in the PIP domain (polar positive [X], negative [X] and neutral [X] residues; non-polar aliphatic [X] and aromatic [X, X and X] residues).

Gene name	SGN[a] scaffold/chromosome	Predicted signal peptide length (aa)	Predicted CDS length (bp)	Prepropeptide length (aa)	PIP domain
***Nicotiana sylvestris* (Nsyl)**					
NsylIDA1	Nsyl_KD945166.1	39	318	105	PIPPSAPSKRHN
NsylIDA2	Nsyl_KD978144.1	32	303	100	PIPPSAPSKRHN
NsylIDA3	Nsyl_KD951180.1	32	243	80	PIPPSAPSKRHN
NsylIDA4	Nsyl_KD977536.1	22	228	75	PIPPSAPSQRHN
NsylIDA5	Nsyl_KD962079.1	30	252	83	PIPASGPSRKHN
***Nicotiana tormentosiformis* (Ntom)**					
NtomIDA1	Ntom_KB972926.1	37	294	97	PIPPSAPSKRHN
NtomIDA2	Ntom_KB954314.1	32	291	96	PIPPSAPSKRHN
NtomIDA3	Ntom_KB969023.1	31	240	79	PIPPSAPSKRHN
NtomIDA4	Ntom_KB956501.1	22	213	70	PIPPSAPSQRHN
NtomIDA5	Ntom_KB958630.1	30	252	83	PIPASGPSRKHN
***Nicotiana tabacum* (Ntab)**					
NtabIDA1A	Ntab-BX_AWOK-SS18147	48	324	107	PIPPSAPSKRHN
NtabIDA1B	Ntab-BX_AWOK-SS9960	37	294	97	PIPPSAPSKRHN
NtabIDA2A	Ntab-BX_AWOK-SS12153	32	303	100	PIPPSAPSKRHN
NtabIDA2B	Ntab-BX_AWOK-SS20685	32	291	96	PIPPSAPSKRHN
NtabIDA3A	Ntab-BX_AWOK-SS473	32	243	80	PIPPSAPSKRHN
NtabIDA3B	Ntab-BX_AWOK-SS2799	31	240	79	PIPPSAPSKRHN
NtabIDA4A	Ntab-BX_AWOK-SS18001	22	228	75	PIPPSAPSQRHN
NtabIDA4B	Ntab-BX_AWOK-SS12176	22	213	70	PIPPSAPSQRHN
NtabIDA5A	Ntab-BX_AWOK-SS18104	30	252	83	PIPASGPSRKHN
NtabIDA5B	Ntab-BX_AWOK-SS9524	30	252	83	PIPASGPSRKHN
***Nicotiana benthamiana* (Nben)**					
NbenIDA1A	Niben101Scf00570	36	270[b]	90	PIPPSAPSK---
NbenIDA1B	Niben101Scf01338	35	306	101	PIPPSAPSKRHN
NbenIDA2A	Niben101Scf23219	32	294	97	PIPPSAPSKRHN
NbenIDA2B	Niben101Scf03368	32	294	97	PIPPSAPSKRHN
NbenIDA3A	Niben101Scf18667	32	243	80	PIPPSAPSKRHN
NbenIDA3B	Niben101Scf01180	32	243	80	PIPPSAPSKRHN
NbenIDA4	Niben101Scf19133	25	240	79	PIPPSAPSQRHN
NbenIDA5A	Niben101Scf03848	30	252	83	PIPASGPSRKHN
NbenIDA5B	Niben101Scf02135	26	240	79	PIPASGPSRKHN
***Solanum lycopersicum* (Slyc)**					
SlycIDA1	SL3.0ch05	36	306	101	PIPPSAPSKRHN
SlycIDA2	SL3.0ch06	30	234	77	PIPPSAPSKRHN
SlycIDA3	SL3.0ch04	27	240	79	PIPPSSPSKRHN
SlycIDA4	SL3.0ch07	34	282	93	PIPPSAPSKRCN
SlycIDA5	SL3.0ch05	29	336	111	LIPPSGPSRRHN
SlycIDA6	SL3.0ch09	26	276	91	PIPPSAPSCRSS
SlycIDA7	SL3.0ch09	27	279	92	PLPPSAPSCRSS
SlycIDA8	SL3.0ch11	28	249	82	PIPASGPSRKHN
***Solanum tuberosum* (Stub)**					
StubIDA1	PGSC0003DMB000000071	27	279	92	PIPPSAPSCRSS
StubIDA2	PGSC0003DMB000000131	28	249	82	PIPASGPSRKHN
StubIDA3	PGSC0003DMB000000243	29	288	95	PVPPSGPSRRHN
StubIDA4	PGSC0003DMB000000410	36	315	104	PIPPSAPSKRHN
StubIDA5	PGSC0003DMB000000420	26	237	78	PIPPSSPSKRHN
StubIDA6	PGSC0003DMB000000461	30	234	77	PIPPSAPSKRHN
StubIDA7	PGSC0003DMB000000592	34	264	87	PIPPSAPSERCN
***Solanum melongena* (Smel)**					
SmelIDA1	Sme2.5_00993.1	30	234	77	PIPPSAPSKRHN
SmelIDA2	Sme2.5_04429.1	28	246	81	PIPPSAPSLRHN
SmelIDA3	Sme2.5_04724.1	27	246	81	PIPASGPSRKHN
SmelIDA4	Sme2.5_06686.1	25	258	85	PIPPSAPSDRCN
SmelIDA5	Sme2.5_08129.1	34	309	102	PIPPSGPSKRHN
SmelIDA6	Sme2.5_09763.1	26	246	81	PVPPSAPSDRCN
***Capsicum annum* (Ca)**					
CaIDA1	PepperUCD10Xch04	27	234	77	PIPPSAPSKRHN
CaIDA2	PepperUCD10Xch06	29	240	79	PIPPSAPSKRHN
CaIDA3	PepperUCD10Xch11	33	309	102	PIPPSGPSKRHN
CaIDA4	PepperUCD10Xch11	35	291	96	PIPPSAPSKRHN
CaIDA5	PepperUCD10Xch11	18	258	85	PIPPSGPSKRHN
CaIDA6	PepperUCD10Xch11	24	315	104	PIPPSEPSPRHN

```
                  *        20         *        40         *        60         *        80
AtIDL2    : ---------MSSRNQRSRITSSFFVSFFTRTILLLLILLLG-FCNGARTNTNVFNSKPHKKHNDAVSS---------- :  58
AtIDL3    : ---------MSSRSHRSRK----YQLTRTIPILVLLLVLLS-CCNGART-TNVFNTSSPPKQKDVVSPPHDHVHHQVQ-- :  63
SlycIDA8  : ---------MISFFRR---------KILVLWMAIILISIFGHFCHGSRSNSQVFNTINNQRNS---------------- :  45
StubIDA2  : ---------MISFFTR---------KVLVLWMTIILISIFGHFCHGSRSNSQVFNTINSQRNS---------------- :  45
SmalIDA3  : ---------MISLFRR---------KVLVLWMAIILISLFG-HCDGSRSNSQVFNPINSQRNS---------------- :  44
Ntab5A    : ---------MISFFRRKVP------LILVFWMAIILITIFG-HCHGSRSSSQVFNPS-SHRNS---------------- :  46
NsylIDA5  : ---------MISFFRRKVP------LILVFWMAIILITIFG-HCHGSRSSSQVFNPS-SHRNS---------------- :  46
NbenIDA5B : ---------MISFFRRKVP------LILVF----ILITIFG-HCHGSRSSSQKFNPS-SQRNS---------------- :  42
NbenIDA5A : ---------MISFFRRKVA------LILVFWMAIILITIFG-HCHGSRSSSQVFNPS-SQRNS---------------- :  46
Ntab5B    : ---------MISFFRRKVP------LILVFWMAIILITIFG-HCHGSRTSSQVFNPS-SQRNS---------------- :  46
NtomIDA5  : ---------MISFFRRKVP------LILVFWMAIILITIFG-HCHGSRTSSQVFNPS-SQRNS---------------- :  46
AtIDL4    : MYPTRPHYWRRRLSINRPQ------AFLLLILCLFFIHHCDAS---RFSSSS-------VFYRNPNYDHSNNTVRRG--- :  61
AtIDL5    : ---------MGNKRIKAMM------ILVVMIMMVFSWRICEADSLRRYSSSSRPQRFFKVRRPNPRNHHHQNQGFNGD-- :  63
SlycIDA2  : ---------MLKKNHNTTL------LIYLL--LVILVVDHHDHHVNAVKNSQVVNVKPLLPSNNNSKSS---------- :  52
StubIDA6  : ---------MLKKNHNRTL------LIYLL--LVILVVDHNDHHANAVKNSQVVNVKPLLPNNNNSKSS---------- :  52
CaIDA2    : ---------MLKKINNIKL------LVYLF--VVILVADHN-HHANAEKNSQVVNVKPLLSSNHNSHKSSL--------- :  53
SmalIDA1  : ---------MLTKIPNTTT------LLVYL--LVVMMLVADNNYANAEKDSQIVNVKPLLPSNKNSKSS---------- :  52
Ntab3A    : ---------MLKRFKNTTI------LVLLLSLHLLLIFVADYHHANATKNSQLFNVKPLPNSHNNSPHTS---------- :  55
NsylIDA3  : ---------MLKRFKNTTI------LVLLLSLHLLLIFVADYHHANATKNSQLFNVKPLPNSHNNSPHTS---------- :  55
NbenIDA3A : ---------MLKRFKNTTI------LVLLLSLHLLLIFLADYHHANATKNSQLFNVKPLPNSHNNSPHTS---------- :  55
Ntab3B    : ---------MLNRIKNTTI------LVLLL-FLLLLIFMADNHHANAAKNSQLFNVKPLTNSHNNSPHKS---------- :  54
NtomIDA3  : ---------MLKRIKNTTI------LVLLL-FLLLLIFMADNHHANAAKNSQLFNVKPLTNSHNNSPHKS---------- :  54
NbenIDA3B : ---------MLKRFKNKTI------LVLLPFLLILLIFMADNYHANATKNSQVFNVKPLPNSHNNSPHRS---------- :  55
SlycIDA3  : --------------MEKMS------IKNTTTISIIFVLVIIIQHAHGASHTQFFKVKPLPISNKN-NKSP---------- :  49
StubIDA5  : --------------MEKMS------IKSTTTISIIFVLVIILH-AHGASHTQFFKVKSLPISNKN-NKSP---------- :  48
CaIDA1    : --------------MEKMS------IKTATYIISIILVLVVIQHAYGARHTQFFKVKPLPKNYNN-KSP---------- :  48
SmalIDA2  : -------------MVKMII------KKTTTISIIFILMMIQLQHAQGASHTQFFKMKSLPIINKNKKNKS---------- :  51
Ntab4A    : -----------------MG------KMRTTLFVVLLLLMVDHAYAARATHTQFLKVQPLHMMNKSHQFS---------- :  46
NsylIDA4  : -----------------MG------KMRTTLFVVLLLLMVDHAYAARATHTQFLKVQPLHMMNKSHQFS---------- :  46
NbenIDA4  : --------------MGKMS------LKTTILFVVLLLLMVDHAYAARATHTQFLKVQPLHMMNKSHQFS---------- :  49
Ntab4B    : -----------------MG------KMRTILFVVLLLLIVGQVYAAR--HTQFLKVKPLHIN--KSQFS---------- :  42
NtomIDA4  : -----------------MG------KMRTILFVVLLLLIVGQVYAAR--HTQFLKVKPLHIN--KSQFS---------- :  42
SlycIDA6  : ---------------MKKQ------SRLFKILLFLFLTTLYYSSSHAITNRKILNLKSRVEIKTSSSVFG---------- :  49
SlycIDA7  : --------------MMNEK------KKFFKSLLFLFLTTLYYSSSYAITNRKILDLKSEIEIKTSSSVFG---------- :  50
StubIDA1  : --------------MMNKQ------SKLSKSLLFLFLTTLYYSSSHAITNRKLLDLKSQIEIKTSSSVFG---------- :  50
AtIDA     : -------------------MAPCRTMMVLLCFVLFLAASSSCVAAARIG---------------ATMEMKKNIKR----- :  41
IDL1      : -------------------MNLSHKTMFMTLYIVFLLIFGSYNATARIGPIKLSETEI-----VQTRSRQEIIGG----- :  51
SlycIDA1  : ---------MAFSFSSSKTLYLSSKLTCLILVISLLFNYGHIVEASRFGRIMMVEEN--------SRIFSSQHMK----- :  58
StubIDA4  : ---------MAFSFSSSKTLYLSSKLICLILVISLLGGYDHIVEASRFGRMMIMEENQ-----EKSRIFSSQHMK----- :  61
CaIDA4    : ---------MASSLSSSKSHYFSSKIICLLLVISLLLVG-YGVEASRFGRKMMIEEN-------NSRLFSSQHMK----- :  58
SmalIDA5  : ---------MAPSLSYSKNLYVSKKLICLVLVISLLVGY--GVEGSRFGRMMMGKKEE-----NSRIFSSQVHLK----- :  59
Ntab1A    : --MASSSSSSSSSSSSSKNKTLYYLICLILAISFLVGYGVEARPGRM----IMEEEE-----ANSRIFSTQHLK----- :  64
NsylIDA1  : ----MASSSSSSSSSSSKNKTLYYLICLILAISFLVGYGVEARPGRM----IMEEEE-----ANSRIFSTQHLK----- :  62
NbenIDA1A : -------MASSSSSSSSKNKTPFYLICLILAISFLVGYGVEARPGRM----IKEEEE-----ANSRIFSTQHLK----- :  59
Ntab1B    : ------MASSSSSSSSSKNKTLYYLICLILAISFLLGYGVEARP----------IEE-----ANSRIFSSQHLK----- :  54
NtomIDA1  : ------MASSSSSSSSSKNKTLYYLICLILAISFLLGYGVEARP----------IEE-----ANSRIFSSQHLK----- :  54
NbenIDA1B : --------MASSSSSSFSKNKTIYYLICLILAISFLLDYGVEARPGRM----IMEGKK-----ANSRIFSTQHLK----- :  58
SlycIDA4  : --------MAYSANSKTLHYISSWKFICLILTLSLVLDHGHGTTCPPTPSRMPRRLKE-----EASRMFSE--------- :  58
StubIDA7  : --------MAYSLNSKTLHYFSSWKFICLILTLSLVLDHGS--ACPPTASRMPRRLKE-----EASRMFSD--------- :  56
SmalIDA4  : --------MASSP---------NLKFMCLILTLSFVLGYGT--TCPPTP---PRSLKE-----EASKMFPE--------- :  44
SmalIDA6  : --------MASSPN------FKTLNFMCLILTLSFVLGYGT--TCPPTP---PWNLKE-----EASKTFPE--------- :  47
CaIDA3    : --------MVYSTNSKT-LHYPSWKFMFLIITLSLVLSYGTATRSMAMTTTTMTTTMNSKEQEEAFRTFSVPNKG----- :  66
CaIDA5    : -------------------------MFLIITLSLVLSYGTATRSMAMTTTTMTTTMNSKEQEEAFRTFSVPNKG----- :  49
Ntab2A    : --------MAYSTNSKT-FHFS-WNFMCFILTLSLVLGYGAAVRTMATATARTTTKKE-----EASGMFSEPVKD----- :  60
NsylIDA2  : --------MAYSTNSKT-FHFS-WNFMCFILTLSLVLGYGAAVRTMATATARTTTKKE-----EASGMFSEPVKD----- :  60
Ntab2B    : --------MAYSTNSKT-FHFS-WNFMCLILTLSLVLGYGAAVRTMATT----TTTKE-----EASGMFSEPVKN----- :  56
NtomIDA2  : --------MAYSTNSKT-FHFS-WNFICLILTLSLVLGYGAAVRTMATT----TTTKE-----EASGMFSEPVKN----- :  56
NbenIDA2B : --------MAYSTNSKT-FYFS-WNFMCLILTLSLVLGYGAAVRSMVATT--TTKNKE-----EASGMFSEPVKD----- :  58
NbenIDA2A : --------MAYSTNSKT-FHFS-WNFICLILTLSLVLGFSAAVRSMVTTT-ATTTTKG-----EASGMFSEPVKD----- :  59
SlycIDA5  : -------------MAYSTTNYSSWKFMYLILTLSLVLGYASSVR-----ISSTMNSKD----EDAYTLFSEPSPKYEDAY :  58
StubIDA3  : -------------MAYSTTNYSSWKFMYLILTLSLVLGYASSVR-----TSSTMNSKE----EDAYRLFSEPSP------ :  52
CaIDA6    : ------------------MAYFSWKFMFLILILSLVLGYTSAARSMAATKTTKMNLKE----KKTSGIFSEPIS------ :  52
AtIDL6    : MARIGALILVLFISISQLASFSTARKFPVGIPSVIDGVIFSGEISAVSKKVTVVGCEGED---DHLTAGYSSYITG---- :  73
AtIDL7    : MAINRSLLLILLFIS---VSLSTARILPG----EFVPVIFSGEIPPVS-KSAVVGCGGEQETKTEYSSFVPEVVAG---- :  68
AtIDL8    : ---------MAKSTYVLVVISFGLLFACVIGTTQDETSRLLWSRPWARGLADSPPQDPHKPTIFGLKPWSP--------- :  62
                    ---------- SIGNAL PEPTIDE ----------                    VARIABLE
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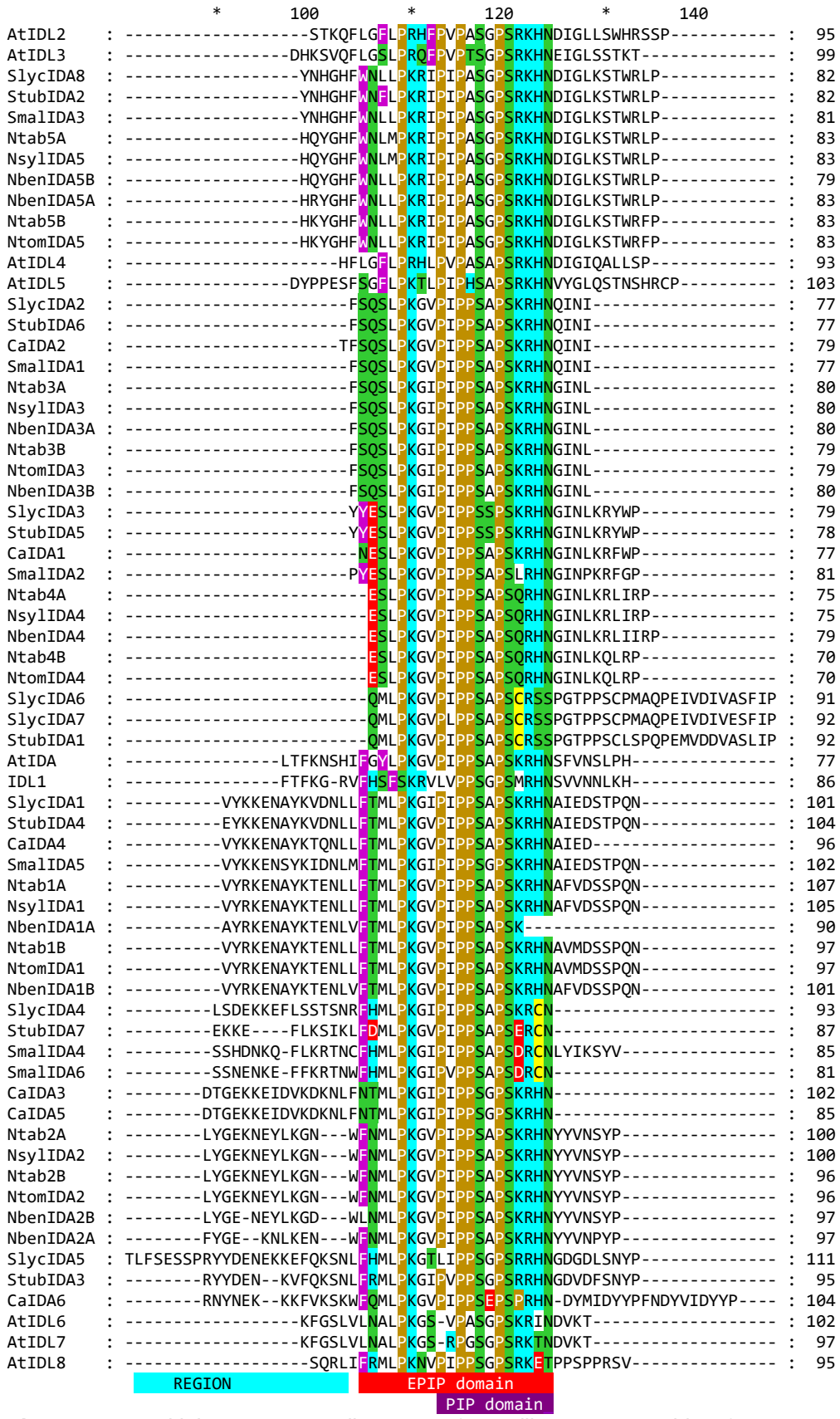


Figure 4.1. Multiple sequence alignment of IDA-like prepropeptides from several species of the Solanaceae family and from Arabidopsis. The CINEMA color scheme is used to show the chemical nature of the amino acid residues in the EPIP domain: (polar positive [X], negative [X] and neutral [X] residues; non-polar aliphatic [X] and aromatic [X, X and X] residues).

The genus *Nicotiana* originated in South America and its members have spread over four continents. This genus consists of diploid species and several allopolyploid species of different ages and ancestry. Thus, cultivated tobacco (*N. tabacum*) is an allotetraploid (2n = 4x = 48) representing a hybridization event involving the diploid species *N. sylvestris* (2n = 2x = 24) and *N. tomentosiformis* (2n = 2x = 24) as their female and male parentals, respectively. This hybridization event is believed to have occurred recently, less than 200,000 years ago (Clarkson et al., 2004; Leitch et al., 2008). The fact that all homeologs of the *IDA*-like family of *N. tabacum* have corresponding counterparts in *N. sylvestris* and *N. tomentosiformis* (Table 4.1 and Figure 4.1) is in line with this observation.

In contrast to cultivated tobacco, *N. benthamiana* has been described as an ancient allotetraploid whose polyploidy level (2n = 4x = 38) likely evolved through genome re-arrangements and fractionation, giving rise to a remarkable descending dysploidy (Leitch et al., 2008). Parentals of *N. benthamiana* are unknown, although it is believed that it comes from a hybridization event that occurred >10 Myr ago between species belonging to the *Sylvestres* and *Noctiflorae* sections of *Nicotiana* (Leitch et al., 2008). In this work, two homeologs were identified in all analyzed genes, except for *NbenIDA4*. Genomic responses to polyploidy are complex in *Nicotiana* species, ranging from small to large genome re-sizing depending on the polyploid age and the similarity of the parental genome donors (Leitch et al., 2008). Reduction in the number of chromosomes in *N. benthamiana* strongly suggests a considerable genome downsizing, probably as a consequence of the old age of the event. The size reduction involves 1 Gb in length relative to cultivated tobacco (4.5 Gb genome size of *N. tabacum*, 3.5 Gb *N. benthamiana*). Therefore, gene loss might explain the absence of a second copy of *NbenIDA4* in these data, rather than a misrepresentation in the draft assembly of the genome used for the analysis. Interestingly, several genetic studies estimated that the genome of *N. tabacum* had lost DNA from its progenitors since polyploidization and that this genomic loss was greater and biased towards the genome of the male parental *N. tomentosiformis* (Skalická et al., 2005; Leitch et al., 2008; Renny-Byfield et al., 2011; Renny-Byfield et al., 2012). Therefore, a similar biased gene loss may have happened in *N. benthamiana* involving the copy of *NbenIDA4* belonging to the parent of the *Noctiflorae* section of *Nicotiana*.

4.2. Phylogenetic relationship among IDA-like prepropeptides in Solanaceae

The phylogenetic relationships among the IDA-like members of the species of Solanaceae studied are grouped in three major clades (Figure 4.2). Clade I (shadowed in green colors) was divided in two subclades. The subclade shadowed in dark green contained the two Arabidopsis prepropeptides involved in floral organ abscission, AtIDA and AtIDL1 (Butenko et al., 2003; Stenvik et al., 2008). The largest subclade grouped members of all eight Solanaceae species studied, as well as AtIDL8, the most divergent IDA-like peptide from Arabidopsis. In this subclade, Solanaceae members are further divided in two major groups. The group shadowed in lime green contained SlIDA1, the IDA-like member of tomato that has been associated with leaf abscission (Tucker and Yang, 2012), other prepropeptides of potato (StubIDA4), eggplant (SmelIDA5) and pepper (CaIDA4), as well as the IDA1 members of the *Nicotiana* species under study: these were NsylIDA1 and NtomIDA1 of the diploid species *N. sylvestris* and *N. tomentosiformis*, respectively, and the two pairs of NtabIDA1 and NbenIDA1 homeolog

prepropeptides corresponding to *N. tabacum* and *N. benthamiana*. The 5′ untranslated regions (5'-UTR) and the predicted coding sequences (CDS) of all these *IDA1* genes from the genus *Nicotiana* showed high degree of conservation (see Supplemental Data S2). The other group shadowed in light green included other prepropeptides from the *Nicotiana*, *Solanum* and *Capsicum* genera, with a small subdivision composed of AtIDL8 together with SlycIDA6, SlycIDA7 and StubIDA1 (Figure 4.2).

A second clade, clade II (shadowed in light orange), is restricted to the Solanaceae family (Figure 4.2). This clade included prepropeptides from the *Nicotiana*, *Solanum* and *Capsicum* genera, but none from Arabidopsis, an observation suggesting that it might have diverged before the irruption of the Brassicaceae family 40 million years ago (Bailey et al., 2006). The third clade, clade III (shadowed in light gold), included AtIDL6 and AtIDL7, two IDA-like members of Arabidopsis that have been associated with processes different than cell separation, such as stress response (Vie et al., 2017). The topology of the clade showed that there was a great diversification in Arabidopsis that generated at least six members, AtIDL2-7. It also included prepropeptides from the *Nicotiana* and *Solanum* genera, but none from *Capsicum*. The Arabidopsis *IDA*-like gene *AtIDL6* grouped in clade III is expressed in rosette leaves and its ectopic over-expression leads to premature abscission of floral organs as does AtIDA (Wang et al., 2017). Thus, AtIDL6 seems to play a similar role to *AtIDA* in the regulation of the cell-wall remodeling. This gene regulates pectin degradation and resistance to bacterial attack in Arabidopsis leaves (Wang et al., 2017) but has not been directly implicated in the regulation of organ abscission.

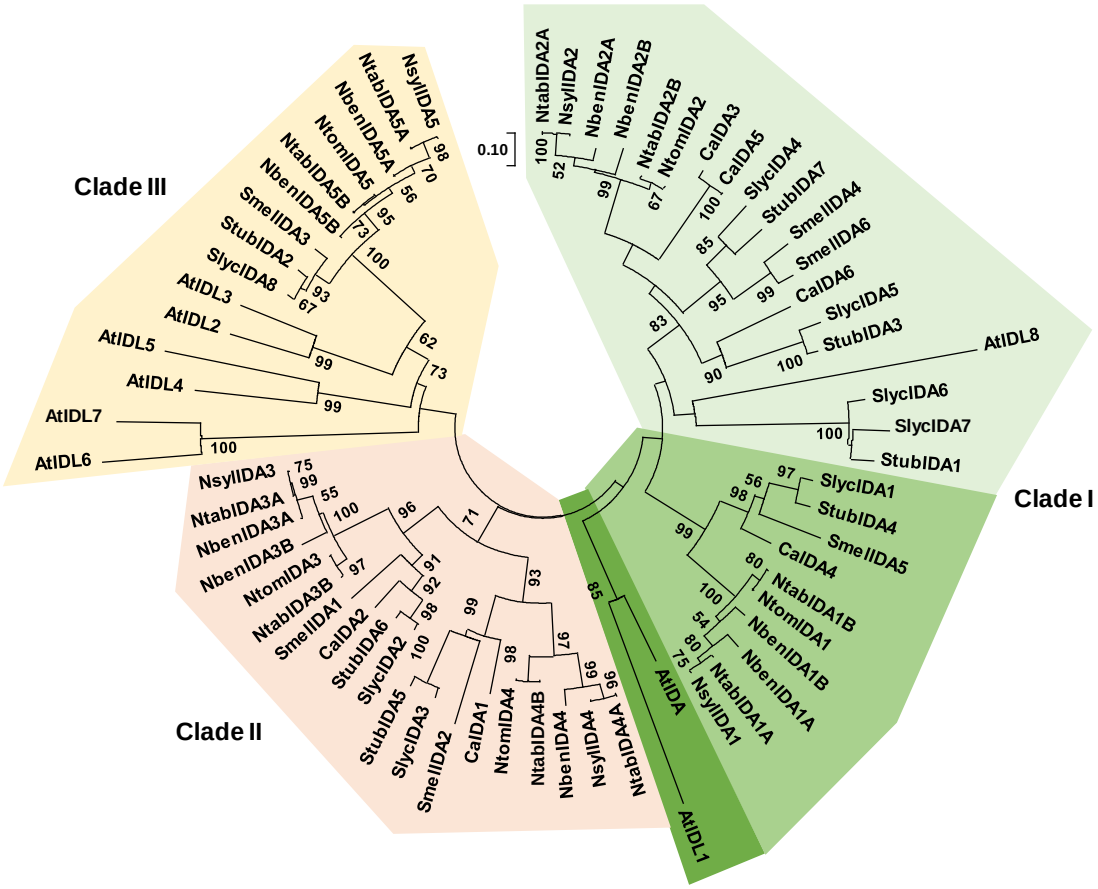


Figure 4.2. Unrooted circular phylogenetic tree of IDA-like prepropeptides of Arabidopsis and relevant species of the Solanaceae family such as *N. sylvestris*, *N. tomentosiformis*, *N. benthamiana*, *N. tabacum*, *S. lycopersicum* (tomato), *S. melongena* (eggplant), *C. annuum* (pepper) and *S. tuberosum* (potato).

4.3. *Cis*-acting regulatory elements in the promoter regions of the *N. benthamiana IDA*-like family

The 5'-UTR region of the *IDA*-like family members of *N. benthamiana* and *AtIDA* and *AtIDL1* of Arabidopsis contained response elements related to several phytohormones: abscisic acid (ABA), methyl jasmonate (MeJa), auxins (AUXs) and gibberellins (GAs) (Figure 4.3). Additionally, response elements related to abiotic (drought) and biotic (defense) stresses were also found. Interestingly, the pair of *NbenIDA1* homeologs contained similar promoter regions carrying response elements to ABA, MeJa and AUX as *AtIDA* in similar locations; these phytohormones have been involved in the abscission process in different ways (for a review, see Estornell et al., 2013). The pairs of *NbenIDA1* and *NbenIDA2* homeologs also carry drought response elements in their promoter regions. On the other hand, *NbenIDA2B*, *NbenIDA3A*, *NbenIDA4*, and the pair of *NbenIDA5* homeologs are characterized by the occurrence of GA response elements (Figure 4.3).

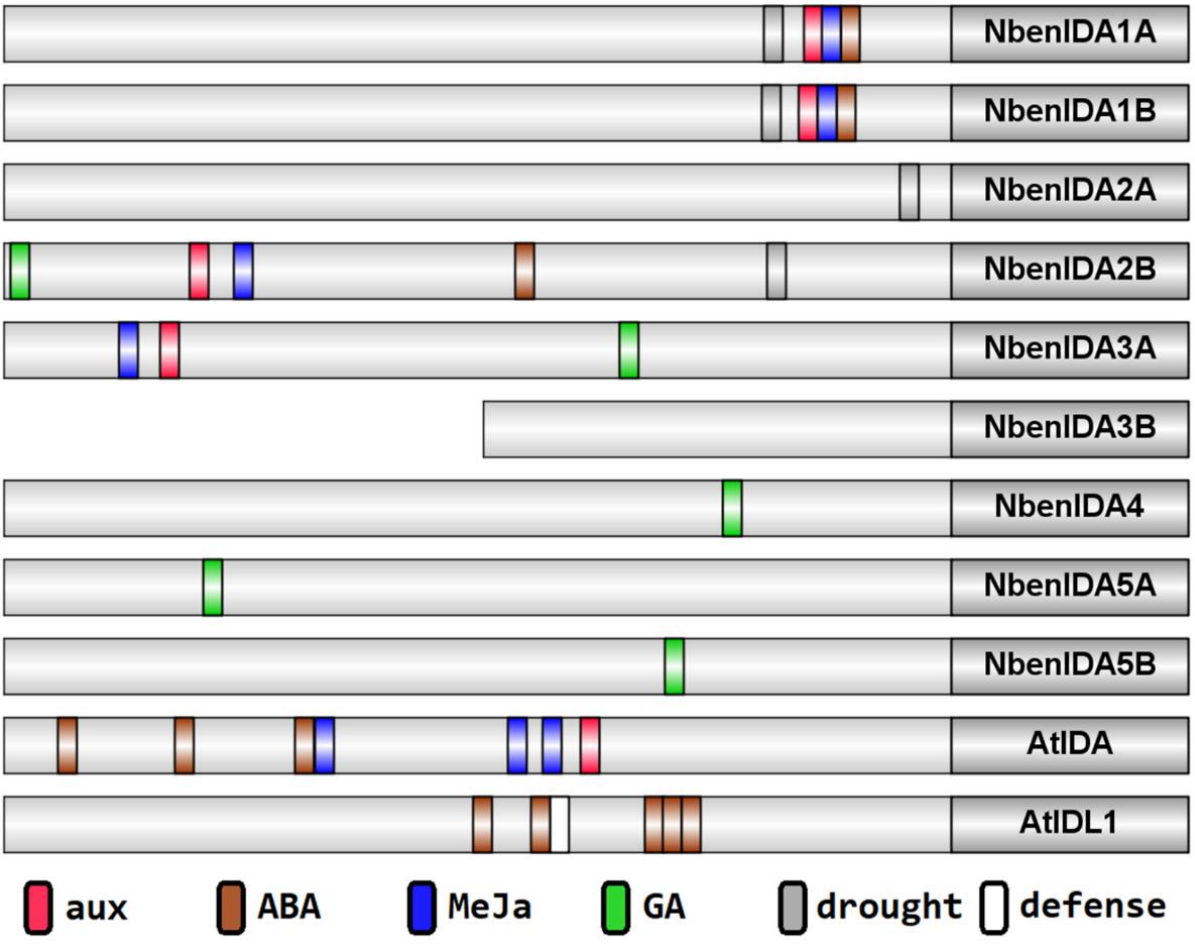


Figure 4.3. Schematic representation of *cis*-acting regulatory elements of the promoter regions of the *N. benthamiana IDA*-like gene family and Arabidopsis *AtIDA* and *AtIDL1*. Light grey boxes represent 1000 bp long promoter regions while dark grey boxes represent the 5' part of the gene. Response elements color scheme: red, auxins (AUX); brown, abscisic acid (ABA); blue, methyl jasmonate (MeJa); green, gibberellins (GA); grey, drought stress (drought); white, defense response (defense). The promoter region of *NbenIDA3B* is 493 bp long since the rest of the sequence is not available yet.

The analyses of the *cis*-acting regulatory elements in the 5'-UTR regions of the *N. benthamiana IDA*-like family and Arabidopsis *AtIDA* and *AtIDL1* (Figure 4.3) failed to identify ethylene response elements, in agreement with the idea that *IDA*-like genes regulating the abscission process are not directly dependent upon ethylene (Butenko et al., 2006; Shi et al., 2019). In contrast, the presence of response elements to AUXs, ABA, MeJa and GAs in the promoter regions of the IDA-like family members of *N. benthamiana* and *AtIDA* and *AtIDL1* suggests that these phytohormones might play a role in regulating the expression of these genes. The occurrence of functional indole-3-acetic acid (IAA) signaling in the abscission zone during organ separation, for instance, has been demonstrated by Basu and co-workers (2013). It has also been determined that ABA and MeJa have abscission-promoting effects, while the role of GAs is not entirely clear (Marciniak et al., 2018; Patharkar and Walker, 2018). However, it has been shown in citrus that flower pollination increased bioactive gibberellin A1 (GA1) levels and reduced ovary abscission, and that the treatment of unpollinated ovaries with gibberellic acid (GA_3) also suppressed ovary abscission (Ben-Cheikh et al., 1997; Mehouachi et al., 2000).
The bioinformatic analyses also indicated that the coding and promoter sequences of the pair of *NbenIDA1* homeologs are highly similar and that promoters share the same hormonal response elements in similar positions, in addition to the same drought response element (Figure 4.3). High conservation of the coding and promoter sequences of *IDA1* duplicated genes in *N. sylvestris*, *N. tomentosiformis* and *N. tabacum* (see Supplemental Data S2) suggests that they may be very important in the regulation of cell separation processes and response to stressful conditions. Furthermore, the pair of *NbenIDA2* homeologs also contains drought stress response elements in their promoter regions (Figure 4.3). Likewise, the coding and promoter sequences of the *IDA1* genes in *N. attenuata*, *N. sylvestris*, *N. tomentosiformis*, *N. benthamiana* and *N. tabacum* are very similar and have the same response elements in the same positions, except *N. attenuata* (see Supplemental Data S2).

4.4. The *HAE*-like gene family in the Solanaceae

The *HAESA* (*HAE*)-like family of Arabidopsis leucine-rich repeat receptor-like kinases (LRR-RLKs) consists of 3 members: *HAESA* (*HAE*), giving its name to the gene family, *HAESA-like1* (*HSL1*) and *HAESA-like2* (*HSL2*). These LRR-RLKs have all been involved in cell separation processes, since *HSL1* mediates *CLE9/10* peptide-derived stomatal development in leaves (Qian et al., 2018) and *HAE* and *HSL2* act redundantly to positively regulate floral organ abscission in Arabidopsis (for a review, see Niederhuth et al., 2013). The involvement of *HAE/HSL2* in organ abscission is fully supported by the non-abscission phenotype showing both *HAE* antisense transgenic lines and the double mutant *hae/hsl2* of Arabidopsis (Jinn et al., 2000; Cho et al., 2008). The role of IDA in the regulation of floral organ abscission in Arabidopsis is dependent on its receptors HAE and HSL2 (Stenvik et al., 2008). HAE/HSL2 do not work alone in the perception of IDA but require the involvement of members of the SOMATIC EMBRYOGENESIS RECEPTOR-LIKE KINASE (SERK) gene family (Meng et al., 2016; Santiago et al., 2016). Downstream of the IDA-HAE/HSL2 receptor complex lies a MITOGEN-ACTIVATED PROTEIN KINASE (MAPK) cascade consisting of MAPK kinase 4(MKK4)/MKK5 and MAPK 3 (MPK3)/MAPK6 (Cho et al., 2008). This phosphorylation cascade leads to the suppression of KNOTTED1-LIKE HOMEOBOX (KNOX) transcription factors, ultimately resulting in the induction of genes encoding cell wall remodeling enzymes, and organ abscission (Shi et al., 2011). In fact, a number of genes encoding cell wall remodeling enzymes are downregulated in the receptacles of the double mutant *hae/hsl2* in comparison to wild type

receptacles, indicating that they are part of the *HAE/HASL2*-dependent abscission process (Liu et al., 2013; Niederhuth et al., 2013b). Since this same transcriptional scenario has been described in receptacles of the *ida2* mutant (Liu et al., 2013), it is then assumed that the expression of cell wall remodeling enzymes should be regulated by the IDA-HAE/HSL2 signaling module. Regarding the involvement of *HAE* or *HSL2* homologs in organ abscission processes in other plant species, it has been recently reported that *LcHSL1*, whose expression is induced in fruit abscission zones in litchi (*Litchi chinensis*) during abscission, is able to rescue the floral organ abscission phenotype in the double mutant *hae/hsl2* of Arabidopsis (Wang et al., 2019a).

Like in the *IDA*-like family, *HAE*-like genes were also searched in relevant genera of the Solanaceae family including several species of *Nicotiana* (*N. sylvestris*, *N. tomentosiformis*, *N. tabacum* and *N. benthamiana*), and other crops of agronomic interest such as tomato (*Solanum lycopersicum*), potato (*S. tuberosum*), eggplant (*S. melongena*) and pepper (*Capsicum annuum*) (Table 4.2 and Supplemental Data S1). A homolog for each of the genes of the *HAE*-like family of Arabidopsis was found in the genomes of *N. syvestris* and *N. tomentosiformis*. The allopolyploid genomes of *N. tabacum* and *N. benthamiana* contained three pairs of homeologs, resulting in *HAE*-like families of six members. The genomes of the remaining Solanaceae species analyzed contained one homolog for each of the genes of the *HAE*-like family of Arabidopsis, excluding *S. lycopersicum* and *S. tuberosum*, which contained two *HSL1* homolog genes. No *HSL2* homolog gene was found in the genome of *S. tuberosum*.

Table 4.2. *HAE*-like gene families in agronomically important species of the Solanaceae family.

Gene name	SGN[a] sequence ID	SGN[a] scaffold/chromosome	Predicted CDS length (bp)	Protein length (aa)
***Nicotiana tabacum* (Ntab)**				
NtabHAE.1	gene_32598 (mRNA_55713)	Ntab-BX_AWOK-SS18352	2955	984
NtabHAE.2	gene_49221 (mRNA_83562)	Ntab-BX_AWOK-SS2766	2424	807
NtabHSL1.1	gene_63539 (mRNA_106017)	Ntab-BX_AWOK-SS4971	2982	993
NtabHSL1.2	gene_63539 (mRNA_106018)	Ntab-BX_AWOK-SS11846	2982	993
NtabHSL2.1	gene_66081 (mRNA_110390)	Ntab-BX_AWOK-SS5522	2967	988
NtabHSL2.2	gene_29102 (mRNA_49768)	Ntab-BX_AWOK-SS17840	2967	988
***Nicotiana sylvestris* (Nsyl)**				
NsylHAE	gene_41518 (mRNA_78595)	Nsyl_KD975002.1	2955	984
NsylHSL1	gene_9122 (mRNA_15487)	Nsyl_KD937107.1	2982	993
NsylHSL2	gene_27949 (mRNA_52300)	Nsyl_KD957655.1	2967	988
***Nicotiana tomentosiformis* (Ntom)**				
NtomHAE	gene_37857 (mRNA_69761)	Ntom_KB968468.1	2424	807
NtomHSL1	gene_25251 (mRNA_45251)	Ntom_KB958681.1	2982	993
NtomHSL2	gene_23142 (mRNA_41082)	Ntom_KB957417.1	2967	988
***Nicotiana benthamiana* (Nben)**				
NbenHAE.1	Niben101Scf09774g00001.1	Niben101Scf09774Ctg001	2894	983
NbenHAE.2	Niben101Scf05190g00001.1	Niben101Scf05190Ctg007	2934	977
NbenHSL1.1	Niben101Scf03169g02005.1	Niben101Scf03169Ctg027	2982	993
NbenHSL1.2	Niben101Scf11552g02006.1	Niben101Scf11552Ctg025	2478	825
NbenHSL2.1	Niben101Scf08143g03001.1	Niben101Scf08143Ctg022	2967	988
NbenHSL2.2	Niben101Scf02417g01010.1	Niben101Scf02417Ctg009	2967	988
***Solanum lycopersicum* (Slyc)**				
SolycHAE	Solyc07g053600.2	SL3.0ch07	2964	987
SolycHSL1.1	Solyc03g006300.1	SL3.0ch03	2988	995
SolycHSL1.2	Solyc02g077630.2	SL3.0ch02	3003	1000
SolycHSL2	Solyc02g091860.2	SL3.0ch02	2970	989
***Solanum tuberosum* (Stub)**				
StubHAE	PGSC0003DMP400016577	PGSC0003DMS000001958	2961	986
StubHSL1.1	PGSC0003DMP400022697	PGSC0003DMS000002817	2988	995
StubHSL1.2	PGSC0003DMP400054963	PGSC0003DMS000000491	3003	1000
***Solanum melongena* (Smel)**				
SmelHAE	–	Sme2.5_02596.1	3036	1011
SmelHSL1	Sme2.5_00787.1_g00015.1	Sme2.5_00787.1	3162	1053
SmelHSL2	Sme2.5_01937.1_g00002.1	Sme2.5_01937.1	2856	951
***Capsicum annum* (Ca)**				
CaHAE	CA07g84190	PepperUCD10Xch07	2952	983
CaHSL1	CA02g15510	PepperUCD10Xch02	3009	1002
CaHSL2	CA02g24590	PepperUCD10Xch02	2955	984

[a] Sol Genomics Network (SGN | https://solgenomics.net/) [Fernandez-Pozo et al., 2015]

4.5. Phylogenetic relationship among HAE-like protein kinases in Solanaceae

The phylogenetic relationships among the *HAE*-like members of the Solanaceae species studied, in addition to those of Arabidopsis, are grouped in two major clades (Figure 4.4). Clade I (shadowed in light gold) contained all the HSL2-like receptor kinases grouping all the proteins of the *Nicotiana* genus into one subclade, while the remaining Solanaceae proteins studied were grouped in another subclade. No Arabidopsis HSL2 homolog was found in the genome of *Solanum tuberosum*. As reported in Arabidopsis (Stø et al., 2015; Shi et al., 2019), clade II included HAE-like and HSL1-like protein kinases, shadowed, respectively, in dark and light green. The phylogenetic relationship between the Solanaceae HAE-like receptor kinases was similar to that described above for HSL2-like receptor kinases. However, the HSL1 homolog of

Capsicum annum (CaHSL1) was grouped together with two tomato (SlycHSL1.2) and potato (StubHSL1.2) receptor kinases, in the *Nicotiana* genus subclade, while the HSL1 homolog of eggplant (SmelHSL1), together with the remaining tomato (SlycHSL1.1) and potato (StubHSL1.1) HSL1-like receptor kinases, were present in another subclade. It has been recently reported that *CaHSL1* was upregulated in pepper leaves by high temperature and humidity and by the application of ABA, but not by the inoculation of *Ralstonia solanacearum*, and downregulated by salicylic acid, MeJa, or ethephon (Guan et al., 2018). The effect of *CaHSL1* silencing by VIGS was a lower tolerance of pepper plants to high temperature and humidity, suggesting that this receptor-like kinase may be involved in stress tolerance (Guan et al., 2018). This hypothesis on the physiological role of *CaHSL1* raises the possibility that *SlycHSL1.2* and *StubHSL1.2* and their *IDA*-like peptide ligands may also be involved in signaling environmental stressful conditions.

Figure 4.4. Unrooted circular phylogenetic tree of HAE-like protein kinases of Arabidopsis and relevant species of the Solanaceae family such as *N. Sylvestris*, *N. tomentosiformis*, *N. benthamiana*, *N. tabacum*, *S. lycopersicum* (tomato), *S. melongena* (eggplant), *C. annuum* (pepper) and *S. tuberosum* (potato).

4.6. Amino acid residues involved in the interaction between IDA mature peptides and HAESA-like receptors

The small signaling peptides of the IDA-like family of Arabidopsis are synthesized as prepropeptides of 70 to 110 amino acids in length, but must follow an obligatory maturation pathway to become active cell signaling elements (for a recent review, see Stührwohldt et al., 2018). The first maturation step is the export of the AtIDA prepropeptide to the endoplasmic reticulum. There, the N-terminal sorting sequence is cleaved off by a signal peptidase resulting in an AtIDA propeptide, as has been reported in other signaling peptide ligands (Olsson et al., 2019a). The following step is the hydroxylation of Pro64 of the AtIDA amino acid sequence by a prolyl-4 hydroxylase while the propeptide is still in the ER or already in the Golgi. This step is key for the activity of the IDA-like peptide ligands because the suppression of the tomato prolyl-4 hydroxylase *SlP4H3* has been reported to delay fruit abscission (Perrakis et al., 2019). The AtIDA propeptide is apparently secreted into the extracellular space, where it undergoes N- and C-terminal proteolytic cleavage to yield a mature 14 amino acids AtIDA peptide, having the optimal length for receptor binding. Specific subtilases (AtSBT5.2, AtSBT4.12 and AtSBT4.13) are involved in the C-terminal processing for maturation cleaving off the propeptide, two amino acids upstream of the PIP domain (Schardon et al., 2016). The C-terminal processing enzyme necessary to yield the mature AtIDA peptide is still unknown. Thus, the mature peptide ligand AtIDA can form a complex with the ectodomain of its specific HAE-like receptor kinases AtHAE and AtHSL2 through the interaction between specific amino acid residues (Santiago et al., 2016). These are Ser62, Pro64 (hydroxylated), Ser65 and Asn69 in the mature AtIDA peptide, while the critical amino acid residues for interaction in the peptide binding pocket of AtHAE are Glu266, Phe289, Ser311, Arg407 and Arg409 (Santiago et al., 2016).

As mentioned above, the amino acid residues Ser62, Pro64, Ser65 and Asn69 of AtIDA are essential in the interaction with the peptide binding pocket of AtHAE (Santiago et al., 2016) and are all conserved in the PIP domains of the Solanaceae IDA-like prepropeptides that may potentially be involved in abscission (Figure 4.5). These amino acid residues are conserved in all members of the *IDA*-like family of Arabidopsis and in most members of the Solanaceae *IDA*-like families (see Figure 4.1). Therefore, other different amino acid residues may be functionally important in abscission. It has recently been suggested that amino acid residues Pro61 and Arg67, which are specific to the AtIDA and AtIDL1 members of the *IDA*-like family of Arabidopsis, may be key in the interaction inside the peptide binding pocket of the receptor kinases (Shi et al., 2019). This hypothesis is based on the fact that although the ectopic overexpression of most of the *IDA*-like genes (*AtIDL1* to *AtIDL5*) resulted in a phenotype very similar to that of *35S:AtIDA* plants, only *AtIDL1* is able to complement the *ida* mutation when its expression was directed under the control of the *AtIDA* promoter (Stenvik et al., 2008). Therefore, the amino acid residues of functional importance in abscission might be those that differ between AtIDA and AtIDL1 and the remaining peptides of the Arabidopsis IDA-like family. It is important to note that many of the members of the *IDA*-like family of Solanaceae also conserve both Pro61 and Arg67 of the AtIDA amino acid sequence (see Figure 4.1). In addition, many of those *IDA*-like genes are not grouped in the lime green subclass of clade I (see Figure 4.2), which encompasses the *IDA*-like genes possibly involved in abscission. Therefore, the hypothesis for Arabidopsis on functionally important amino acid residues in abscission may perhaps be extended, considering the results obtained in Solanaceae, to the entire

surroundings of the PIP domain and not only to Pro61 and Arg67 of the AtIDA amino acid sequence.

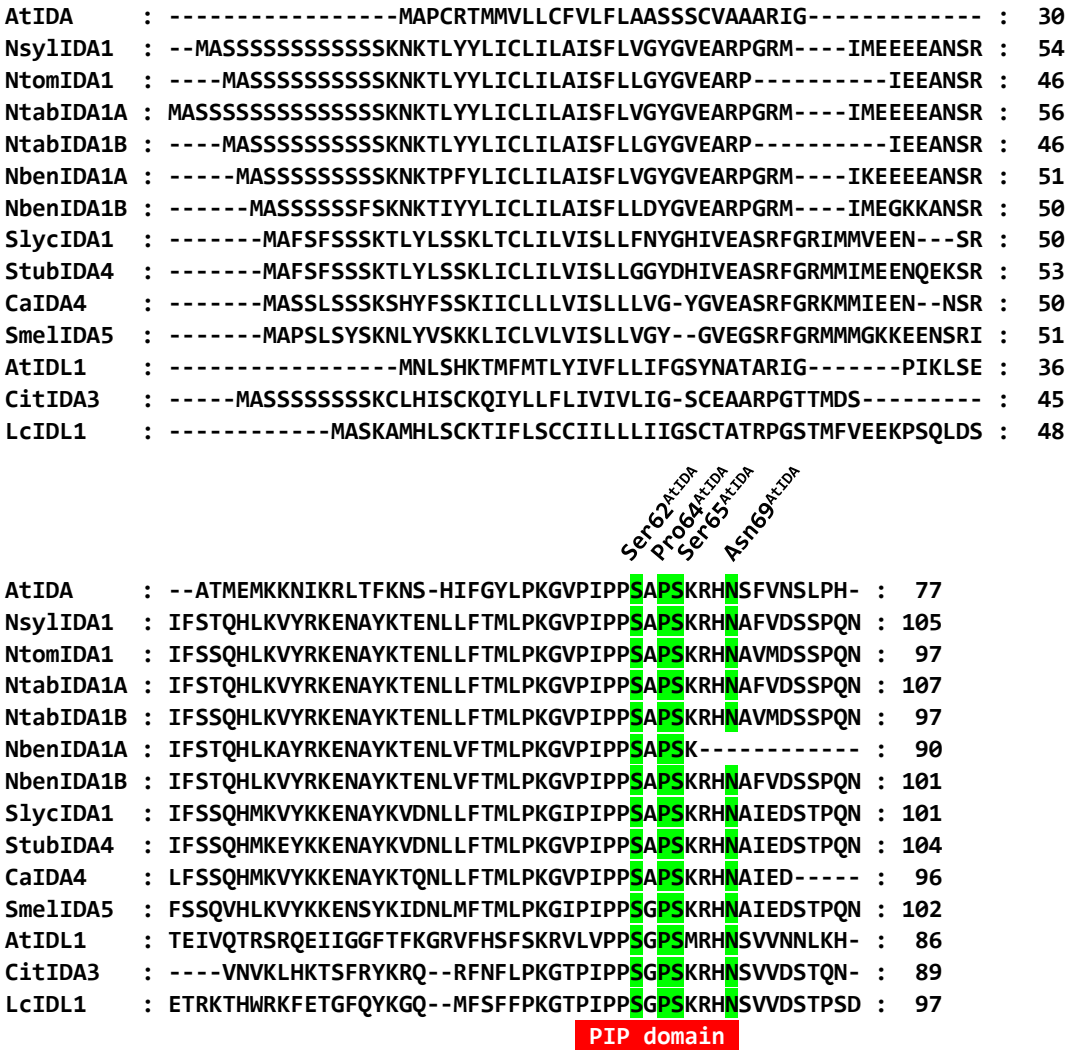


Figure 4.5. Multiple sequence alignment of selected Arabidopsis and Solanaceae IDA-like prepropeptides contained in clade I (see Figure 4.2) together with the citrus (CitIDA3) and litchi (LcIDL1) prepropeptides replacing the function in abscission of IDA in Arabidopsis (Estornell et al., 2013; Ying et al., 2016). The PIP domain amino acids that directly bind to the ectodomain of the LRR-RLKs HAE/HSL2 are shadowed in green.

Regarding the amino acid residues inside the peptide binding pocket of AtHAE and AtHSL2 key to the interaction with AtIDA (Figure 4.6), there are five critical amino acid residues for binding (Glu266, Phe289, Ser311, Arg407 and Arg409) and others that are also involved, although they are secondary to ligand-receptor binding (Santiago et al., 2016). These are: Ser147, Tyr196, Trp218, Asn240, Asp242, Gln264, Arg288, Asp290, Asn313, Phe315, Lys337, Phe339, Asp361, Ser363, Tyr364 and Ile385 of the AtHAE amino acid sequence (Figure 4.6). All critical amino acid residues in the peptide binding pocket are conserved between AtHAE and both NbenHAE receptor kinases, while Arg407 is replaced by Tyr417 in AtHSL2 amino acid sequence and also the HSL2 receptor kinases NbenHSL2.1, NbenHSL2.2 and the litchi receptor kinase LcHSL2 involved in fruit abscission (Wang et al., 2019a) (Figure 4.6). In line with the secondary role of the other amino acid residues in the ligand-receptor bond, the other positions involved in the interaction are much less conserved.

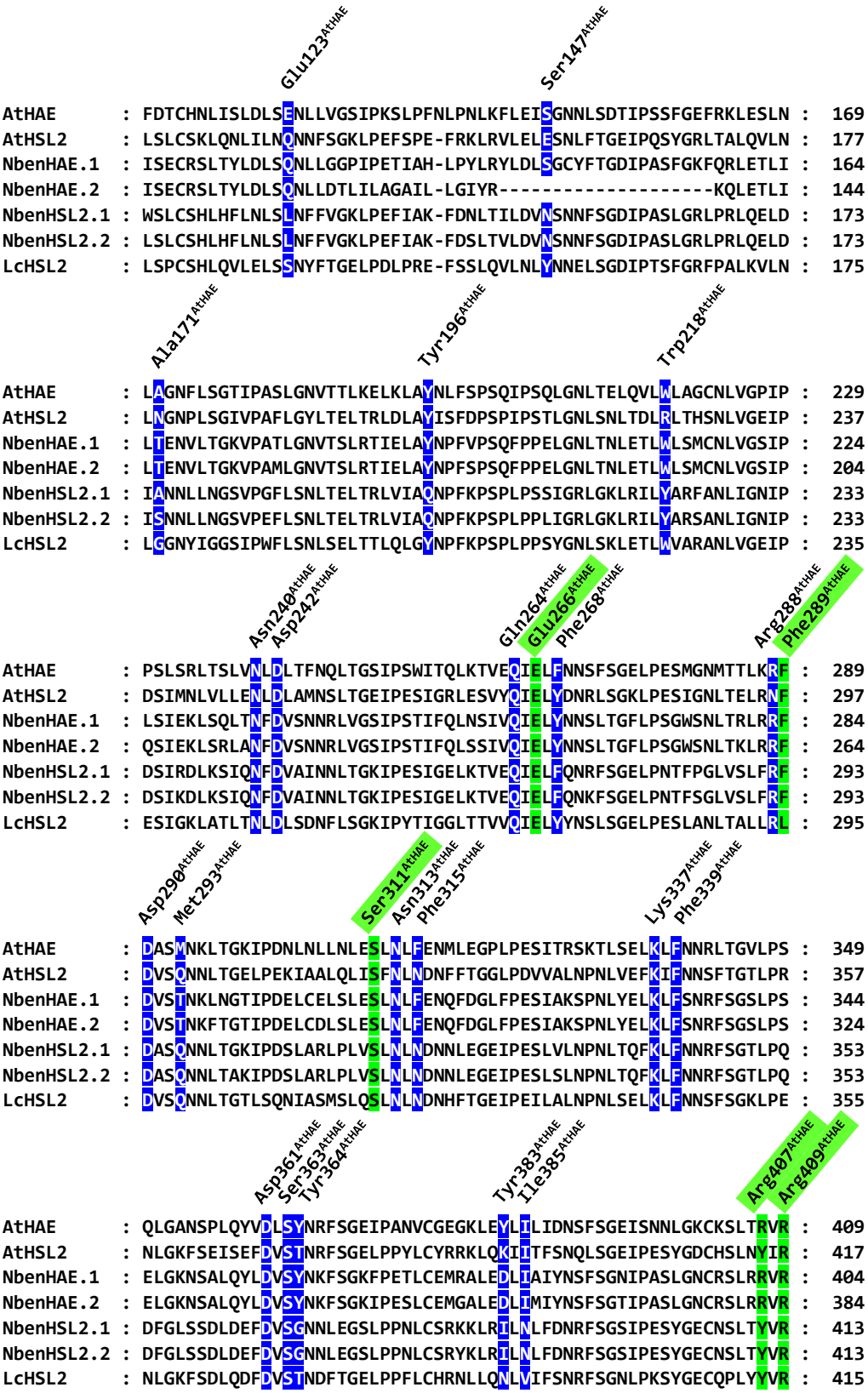


Figure 4.6. Multiple sequence alignment of selected Arabidopsis and *N. benthamiana* HAE-like protein kinases (see Figure 4.4) together with a litchi protein kinase (LcHSL2) replacing the function in abscission of HAE/HSL2 in Arabidopsis (Wang et al., 2019a). Critical IDA-interacting amino acid residues in the binding pocket of HAE LRR-RLKs are shadowed in green whereas other amino acid residues also interacting with IDA are shadowed in blue.

The receptor-like protein kinases of the HAE-like family function in Arabidopsis in the perception of various peptide ligands of the IDA-like family to activate cell separation processes such as organ abscission (Jinn et al., 2000; Cho et al., 2008; Butenko et al., 2014), emergence of lateral roots (Kumpf et al., 2013; Zhu et al., 2019), response to pathogen attack (Wang et al., 2017), root cap sloughing (Shi et al., 2018) and stomata differentiation (Qian et al., 2018). Only in certain species of agronomic interest such as soybean (Tucker and Yang, 2012), citrus (Estornell et al., 2015), oil palm (Stø et al., 2015), and litchi (Ying et al., 2016; Wang et al., 2019a), genes of the *IDA*-like and *HAE*-like families with potential involvement in organ abscission have been identified. Of these four examples, just the litchi receptor-like protein kinase *LcHSL2* has been shown to be a functional abscission homolog of Arabidopsis *AtHSL2* (Wang et al., 2019a). All critical amino acid residues in the peptide binding pocket are conserved between AtHAE and both NbenHAE receptor-like kinases, and between AtHSL2 and LcHSL2 and both NbenHSL2 receptor-like kinases (Figure 4.6), suggesting that the two pairs of NbenHAE and NbenHSL2 homeologs of *N. benthamiana* might bind IDA-like peptides and, therefore, might be functional in organ abscission.

4.7. Expression patterns of *IDA*-like and *HAE*-like genes in *Nicotiana benthamiana* during growth and abscission

The expression patterns of all members of the *IDA*-like family of ligand peptides and their suspected *HAE*-like receptors in *N. benthamiana* plants were analyzed for their potential organ and tissue expression specificity. The selected plant material included different vegetative tissues of a plant in active growth (apical buds, young and mature leaves, nodes and internodes, and roots), as well as reproductive tissues (anthers, styles, stigmas, and fruits, called capsules) at different flower developmental stages based on the growth and development of the corolla. Tissue samples from the base of the corolla tube were also included in the gene expression analysis, a tissue that in cultivated tobacco (*N. tabacum*) has been shown to respond to the abscission process (Wu et al., 2012).

Plants of *N. benthamiana* used in this study were derived from germinated seeds of a laboratory strain provided by Dr. José Guerri and Dr. Karelia Velázquez (IVIA-Centro de Protección Vegetal y Biotecnología, Moncada [Valencia], Spain). In these plants, solitary flowers arise from the leaf axils and from the main and secondary stem internodes of the *N. benthamiana* plants. They are pentamerous flowers, where the perianth is composed of a calyx of five sepals, and five fused petals forming a sympetalous tubular corolla capped by a five-lobed limb (Figures 4.7 and 4.8B). The five stamens are epipetalous and the gynoecium is bicarpellate and formed by a short bilocular ovary with central placentation. From the apical portion of the ovary starts an elongated style capped by a round flat stigma which is inserted into the upper half of the corolla tube. The internal floral structures show homostylity, with styles of uniform length and equal to that of the stamens.

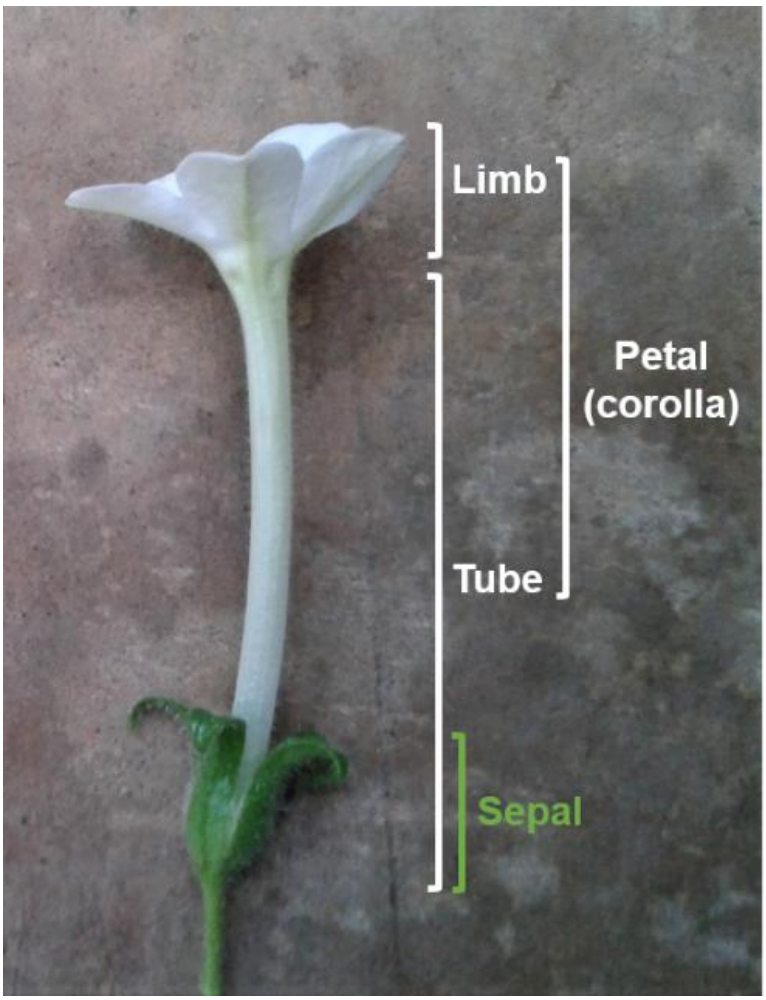


Figure 4.7. External parts of the flower of *Nicotiana benthamiana*.

Table 4.3. Morphological markers of the flower development of *N. benthamiana*.

Developmental stage	Morphological markers
1	Corolla tube bulge above calyx; corolla limb tips closed
2	Corolla tube bulge fully elongated, enlarging horizontally and cup-shaped; corolla limb tips closed; anther tapetum degenerated and connective tissue separating the pollen sacs starting to degrade[a]
3	Onset of anthesis; corolla limb halfway open; corolla limb lobes expanding horizontally; bilocular anthers with pollen grains filling the locules[a]
4	Whole open flower; corolla limb lobes fully expanded; sharp pinwhite border at top of tube cup-bulge; anthers dehisce along the stomium
5	Onset of corolla senescence; margins of the corolla limb lobes curl inwards; corolla tube shows an appreciable loss of turgidity
6	Corolla limb completely contracted and brown; corolla tube is drying
7	Corolla death; corolla tube is completely dried and brown; corolla tube can be easily detached by its base

[a] Anatomical parameters of anther development taken from reported *N.tabacum* data (Koltunow et al., 1990)

The life span of the corolla can be divided into seven stages associated with the development of the *N. benthamiana* flower (Table 4.3). These stages include corolla tube elongation, corolla opening, and corolla collapse and senescence (Figure 4.8A). The corolla tube is fully elongated between flower stages 1 and 2 and flower anthesis extends between stages 3 and 4. It is also between stages 3 and 4 of flower development that anther dehiscence occurs (Figure 4.8B). The senescence of the corolla begins in the floral stage 5 and extends until stage 7. The senescence process is characterized by a gradual loss of corolla tube turgidity and the emergence of a noticeable brown ring at the base of the corolla tube (Figure 4.8C). This brown basal ring marks a band of apparently low mechanical resistance, a potential abscission zone through which the corolla will detach from the flower receptacle. The fruits in the Solanaceae family are predominantly capsules and berries, with dry capsules in the subfamily Nicotianoideae (Knapp, 2002). The enlargement of the capsule also contributes to the disintegration of the base of the corolla tube and their shedding of the flower receptacle. Thus, unlike the free-petaled choripetalous corollas of, for example, Arabidopsis, in which the petals are separated by their attachment point to the receptacle (McKim et al., 2008), in the sympetalous corollas of *Nicotiana* flowers the cell separation process seems to occur at the base of the corolla tube (Wu et al., 2012; Figure 4.8C). The flower corolla can be easily separated in flower stage 7 by a gentle pulling out. In later stages, structural damage to the base of the corolla tube is enhanced by capsule development until it is completely detached from the flower.

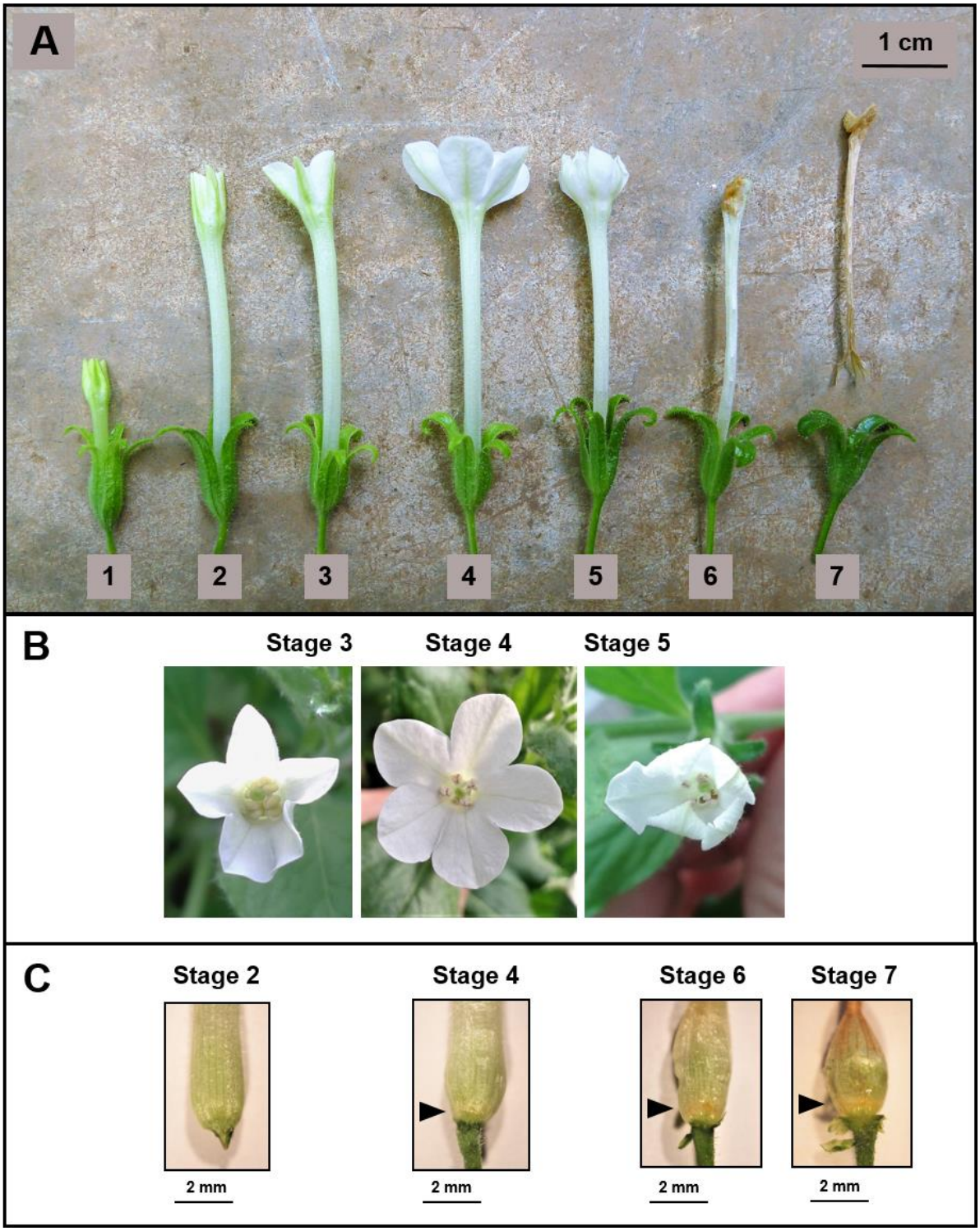


Figure 4.8. Corolla developmental stages of the flower of *Nicotiana benthamiana*. **(A)** The corolla life span is divided in seven stages which include elongation of the corolla tube [stages 1 and 2], corolla opening [stages 3 and 4] and corolla collapse and senescence [stages 5, 6 and 7]. **(B)** Dehiscence of the five anthers occurs during the opening of the corolla between stages 3 and 4, and are completely dehiscent by stage 5, when corolla limb lobes curl inwards. **(C)** The basal part of the corolla tube is swollen and turgid in stage 2, while it begins to lose turgidity in stage 4. A brown ring appears at the base of the corolla tube at stage 4 and is clearly visible at the base of the senescent corolla at stage 6 (see arrowheads). The base of the corolla tube begins to lose its structural integrity at stage 7, which allows the corolla to be separated from the flower by gentle pulling out.

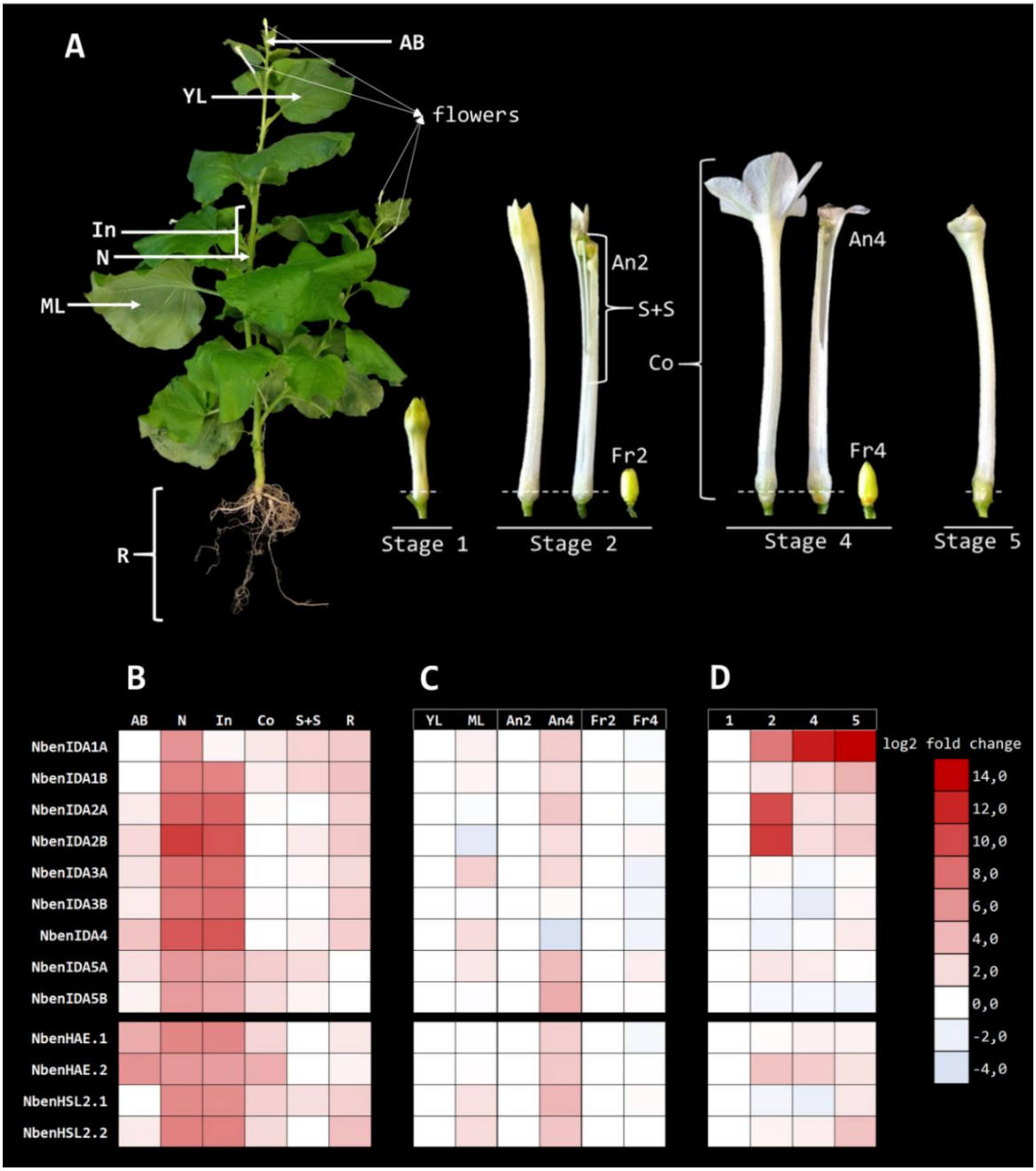


Figure 4.9. Expression patterns of *IDA*-like and *HAE*-like genes based on quantitative real-time PCR in several organs and tissues of *N. benthamiana* at different stages of flower development. **(A)** Floral organs (sepals were removed), capsules (fruits) and vegetative tissues employed for gene expression analysis. Samples of whole corolla and the ensemble formed by the style and the stigma were collected in stage 4 of flower development. Dashed lines mark the tissue collected from the base of the corolla. **(B)** Gene expression levels in apical buds (AB), nodes (N), internodes (In), whole corolla (Co), the ensemble formed by the style and the stigma (S+S) and roots (R) relative to the lowest expression level of each gene. **(C)** Gene expression patterns in leaves, anthers and capsules (fruits). Gene expression levels were relativized to that at the earliest developmental stage in every organ (YL, young leaf; An2, anthers at stage 2; Fr2, capsule (fruit) at stage 2, respectively). **(D)** Gene expression patterns in the corolla base during flower developmental stages 1, 2, 4 and 5: Gene expression levels were relativized to that at flower stage 1. Gene expression levels were normalized with respect to those of *NbenPP2A* gene, applying the $2^{-\Delta\Delta Ct}$ method. Relative gene expression levels (log2 fold change) are given next to the color scale column. Upregulation and downregulation of gene expression is shown by red and blue color, respectively.

The plant material selected for gene expression analyses is shown in the panel A of Figure 4.9. In this figure, panel B shows gene expression relative to the lowest expression level of each gene of IDA-like and HAE-like homeolog in several tissues including apical buds, nodes, internodes, the whole corolla, the ensemble formed by the stigma and the style, and roots. Panel C shows the expression pattern of each *IDA*-like and *HAE*-like homeolog in leaves, anthers and capsules (fruits) relative to that at the earliest developmental stage in every organ. Panel D shows the expression patterns of each homeolog at the corolla base in flower developmental stages 2, 4 and 5, relative to developmental stage 1. Virtually all members of the *IDA*-like family of *N. benthamiana* were mainly expressed in nodes and internodes, although *NbenIDA1A* expression levels were not especially high in internodes (Figure 4.9B). No changes in the expression patterns of *IDA*-like homeolog genes were observed in leaves and capsules (fruits) (Figure 4.9C), but the expression level for all of them, except *NbenIDA3B* and *NbenIDA4*, showed a tendency to increase between closed and dehiscent anthers (Figure 4.9C). Interestingly, expression of both *NbenIDA1* homeologs at the base of the corolla tube increased with the stage of development of the tissue, in parallel to the progress of the abscission process (Figure 4.9D). The expression pattern of *NbenIDA1A* was similar to that detected in *NbenIDA1B*, although at a higher level. The expression levels of the *NbenIDA2* homeologs were transiently high in flower stage 2, when the corolla tube is fully elongated and the limb lobes are still closed, to return at flower stages 4 and 5 to almost the basal expression level (Figure 4.9D).

The highest expression levels of the putative receptors of the IDA-like peptides, *NbenHAE.1*, *NbenHAE.2*, *NbenHSL2.1* and *NbenHSL2.2*, were also registered in nodes and internodes (Figure 4.9B). Additionally, their expression levels also showed a tendency to increase between closed and dehiscent anthers (Figure 4.9C), and a slight increase was observed at the corolla base associated with corolla development (Figure 4.9D).

As described for *IDA*-like families in other species (Vie et al., 2015), the different members of the *N. benthamiana* family are also expressed in multiple plant tissues (Figure 4.9). This is not a surprise since the *IDA*-like signaling peptides, as cell-to-cell communication elements, function in several cell separation events, including lateral root emergence and root cap sloughing (Kumpf et al., 2013; Shi et al., 2018). Interestingly, in actively growing plants of *N. benthamiana*, the highest expression level of most members of the *IDA*-like family was found in nodes and internodes (Figure 4.9B). It is worth mentioning that the promoter regions of *NbenIDA2B*, *NbenIDA3A*, *NbenIDA4*, *NbenIDA5A* and *NbenIDA5B* genes, contain GAs response elements (see Figure 4.3), and that these hormones are pivotal regulators of stem growth (Rizza and Jones, 2019). Moreover, all *HAE*-like genes analyzed also show higher expression levels in nodes and internodes, in parallel with the pattern observed for the *IDA*-like genes. These expression patterns might be linked to the formation of vascular bundles, and to both cell elongation and cell division associated with the process of stem elongation, implying cell wall remodeling.
The *IDA*-like genes *NbenIDA1A* and *NbenIDA1B* may be involved in the abscission process (Figure 4.9D). This suggestion is also supported by the gene expression patterns found at the corolla base of the flowers during the process of natural abscission (Figure 4.9D). Similarly, there seems to be a correlation between the expression of the *IDA*-like genes and that of their putative receptors of the *HAE*-like family, *NbenHAE.1*, *NbenHAE.2* and *NbenHSL.2.2* (Figure 4.9D), that also increased during the last phases of the corolla abscission.

Our gene expression data showed that, while most pairs of homeologs showed similar expression patterns, some of them exhibited divergence in certain organs and tissues studied (see Figure 4.9). This might be linked to the frequent observation that some duplicated genes, after a whole genome duplication event, evolve to undertake different functions or partition the function of the ancestral gene in a process of subfunctionalization. This process can include epigenetic, coding sequence or promoter modifications that alters regulatory mechanisms (e.g. silencing) and give rise, for example, to differential expression levels or tissue specificities. Subfunctionalization becomes more relevant when gene dosage is not an adaptive advantage for the polyploid (Force et al., 1999). Therefore, our gene expression data might be revealing a putative subfunctionalization for the homeolog pairs *NbenIDA1* at the corolla base and *NbenIDA3* in leaves and anthers. We took special care in primer specificity during qPCR assays in order to distinguish between both homeologs, since gene expression artifacts may be recurrent among genes derived from genome duplicated areas due to high sequence similarity.

4.8. Expression patterns of *IDA*-like genes in *Nicotiana benthamiana* during water stress

The presence of drought response elements in the promoter regions of some particular *IDA*-like members, e.g. *NbenIDA1A*, *NbenIDA1B*, *NbenIDA2A* and *NbenIDA2B* (Figure 4.3), suggested that their expression might be regulated by the water status of the plant. Therefore, we exposed actively growing plants of *N. benthamiana* to 6 (mild stress) and 8 (severe stress) days of water stress, and the expression levels of all members of the *IDA*-like family in roots and leaves were determined (Figure 4.10). The expression level of the pair of *NbenIDA1* homeologs dramatically increased in leaf blades of plants subjected to severe water stress. In contrast, this condition resulted in higher increases in transcripts belonging of both *NbenIDA2* homeologs in roots, indicating differential roles of this gene family in response to water stress. Changes in the expression of the rest of genes were of minor relevance, although it is worth to mention that these members tended to repress their expression levels in roots of plants subjected to water stress, whereas *NbenIDA5A* expression was also reduced in stressed leaves.

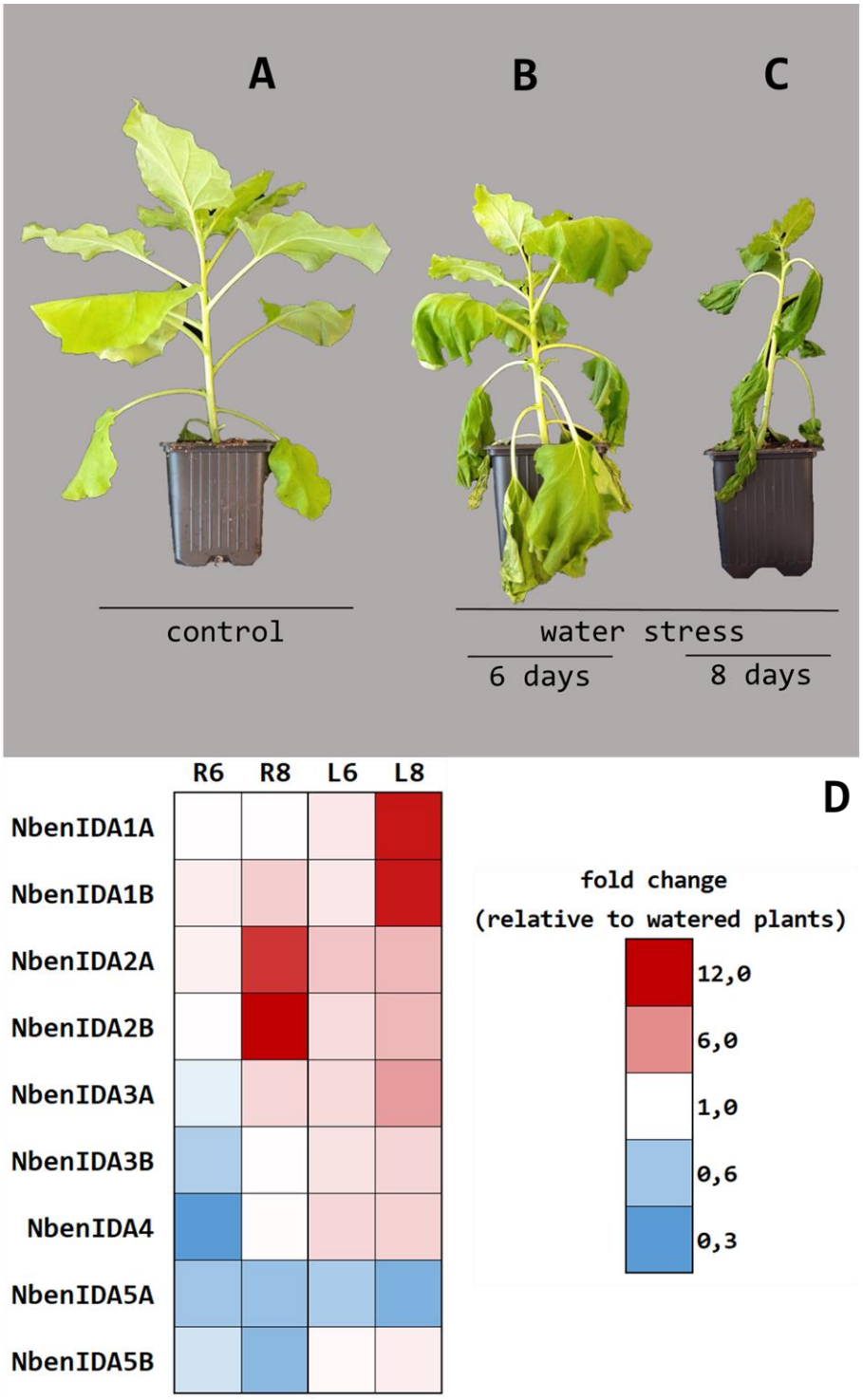


Figure 4.10. Expression patterns of *IDA*-like genes based on quantitative real-time PCR in control and water stressed plants of *N. benthamiana*. General appearance of a well-watered plant **(A)** and plants subjected to water stress for 6 days **(B)** and for 8 days **(C)**. Expression patterns in roots (R) and mature leaves (L) of water stressed plants during 6 or 8 days **(D)**. Expression levels were calculated through the $2^{-\Delta\Delta Ct}$ method, normalized to that of *NbenPP2A* gene and relativized to gene expression in control (watered) plants. For each stressed organ the appropriate reference was used (well-watered leaf or root). Expression levels relative to watered plants (fold change) are given next to the color scale. Red, white and blue colors indicate, respectively, gene induction (values over 1), unchanged (values close to 1), and repression (values under 1), all of them regarding to that of the *NbenPP2A* gene in the relevant watered (control) organ.

It has been reported that IDA signaling peptides can certainly regulate important developmental processes as well as plant responses to environmental conditions (Vie et al., 2015, 2017; Wang et al., 2017). A recent genetic and biochemical study reported that an Arabidopsis dominant mutant named *sbt4.13-1D* showing over-expression of the *SBT4.13* subtilase, was tolerant to cytosolic acidification induced by organic acids (Bissoli et al., 2020). The addition of weak organic acids to the culture medium causes cytosolic acidification, a consequence of many abiotic stresses (Menegus et al., 1989; Gruwel et al., 2001; Fischer and Kaldenhoff, 2008; Barnes et al., 2019). Cytosolic acidification induces the production of reactive oxygen species (ROS), and ROS production is greatly reduced in *sbt4.13-1D* mutant (Bissoli et al., 2020). Therefore, *SBT4.13* subtilase might somehow be involved in the regulation of ROS homeostasis and antioxidant gene expression. Intriguingly, *SBT4.13* participates in the proteolytic processing of Arabidopsis IDA propeptide, which is fundamental to get a mature active peptide (Schardon et al., 2016), suggesting a participation of the IDA signaling peptide in the modulation of stress-induced oxidative damage. Our data indicate that in the allopolyploid *N. benthamiana*, the two pairs of *NbenIDA1* and *NbenIDA2* homeologs are differentially involved in the responses to drought stress, while only *NbenIDA1* homeologs are apparently implicated in the natural process of corolla abscission. These data suggest that IDA-like signaling peptides can play different biological roles in various tissues and under distinct abiotic conditions.

4.9. Conclusions

In this section, the *IDA*-like and *HAE*-like gene families of different Solanaceae species, *S. lycopersicum, S. melongena, C*. *annuum,* S. *tuberosum,* and four species of the genus *Nicotiana*, *N*. *sylvestris, N. tomentosiformis, N. benthamiana,* and *N. tabacum* were identified and their phylogenetic relationships were also determined. In the allopolyploid *N. benthamiana,* specific analyses of the *cis*-acting regulatory sequences and the examinations of the gene expression patterns of the *IDA*-like family have identified putative candidate *IDA*-like genes implicated in corolla abscission and in the response to water stress. The results suggest that the *NbenIDA1* and *NbenHAE* pairs of homeologs might be involved in the natural process of corolla abscission. Interestingly, they also show specific differential expression under water stress conditions. *NbenIDA1* homeologs are highly expressed in stressed leaves, while *NbenIDA2* homeologs, especially *NbenIDA2B*, are highly expressed in stressed roots. In addition, nodes and internodes are the tissues with the highest expression of the *IDA*-like and *HAE*-like genes in normal active growing plants, suggesting that these peptides are also essential during stem growth and development. These results add new evidence that the functional module formed by IDA-like peptides and its receptor kinases as defined in Arabidopsis, might be conserved in Solanaceae.

5

Silencing and overexpression of *INFLORESCENCE DEFICIENT IN ABSCISSION* and *HAESA* receptor kinase in flowers of *Nicotiana benthamiana*: effects on corolla abscission

The interaction of the hormonal peptide INFLORESCENCE DEFICIENT IN ABSCISSION (IDA), a pair of redundant receptor-like protein kinases, HAESA (HAE) and HAESA-LIKE2 (HSL2), and SOMATIC EMBRYOGENESIS RECEPTOR-LIKE KINASE co-receptors regulates abscission of floral organs and cauline leaves in Arabidopsis (for recent reviews, see Patharkar and Walker, 2018; Shi et al., 2019). In addition to Arabidopsis, *IDA*-like genes have also been identified in a number of crop species. Thus, it has been reported that some of them were highly expressed in AZs in tomato (Tucker and Yang, 2012), soybean (Tucker and Yang, 2012), oil palm (Stø et al., 2015), citrus (Estornell et al., 2015), litchi (Ying et al., 2016) or yellow lupine (Wilmowicz et al., 2018) and, as it has been described in the previous section, at the base of the corolla tube of *N. benthamiana* flowers. These observations strongly suggest that *IDA*-like genes might conserve in other species the same function that *IDA* exerts in Arabidopsis, regulating cell separation during organ abscission. It has been also shown that synthetic IDA peptides were able to induce early floral organ abscission in Arabidopsis (Stenvik et al., 2008), and abscission of flowers, mature fruits and leaves in yellow lupine, oil palm and Poplar, respectively (Wilmowicz et al., 2018; Tranbarger et al., 2019). Additionally, IDA homologs of citrus (*CitIDA3*) and litchi (*LcIDA1*) heterologously expressed in Arabidopsis were functional, producing earlier floral organ abscission and rescuing the *ida2* abscission deficiency (Estornell et al., 2015; Ying et al., 2016). Similarly, the ectopic overexpression of a *HAE*-like homolog of litchi, *LcHSL2*, completely rescued abscission of floral organs in the Arabidopsis double mutant *hae/hsl2* (Wang et al., 2019a). Finally, the ectopic expression of *LcKNAT1*, the litchi homolog of Arabidopsis *BREVIPEDICELLUS* (*BP*) / *KNOTTED-LIKE FROM ARABIDOPSIS*

THALIANA1 (*KNAT1*), prevented the abscission of flowers and floral organs in tomato and Arabidopsis, respectively (Zhao et al., 2020).

Transient expression studies and virus-induced gene silencing (VIGS) are feasible to be performed in *N. benthamiana* in order to conduct functional studies. Actually, *N. benthamiana* is one of the most commonly used model plant organisms to perform host-pathogen interaction studies due to its hypersensitivity to viruses and other pathogenic agents (Goodin et al., 2008). In this section, the corolla abscission behavior of *N. benthaniana* flowers in response to VIGS-based silencing and/or overexpression of the pairs of *NbenIDA1* and *NbenHAE* homeologs is described. This study was designed to elucidate whether the IDA-HAE/HSL2 module regulating organ abscission in Arabidopsis is conserved in other angiosperms.

5.1 Silencing and overexpression of *IDA*-like and *HAE*-like genes using a viral vector based on *Citrus leaf blotch virus*

Virus-induced gene silencing (VIGS) has allowed to elucidate the function of many genes involved in a wide range of plant development processes, including organ abscission. Dissolution of the middle lamella in AZs of different aerial organs of tomato plants occurs in response to cell wall hydrolysis enzymes and remodeling proteins (for a review, see Ito and Nakano, 2015). The importance of expansins (EXPs), endo-β-1,4-glucanases/cellulases (CELs) and polygalacturonases (PGs) in tomato leaf abscission was demonstrated by VIGS approach using *Tobacco rattle virus* (*TRV*)-based vectors (Jiang et al., 2008). In this study, it was shown that the silencing of *LeEXP11* and *LeEXP12*, and *LeCEL1* and *LeCEL2*, had no detectable effect on the force required to produce petiole abscission, while a fragment of *TAPG1* in the silencing vector delayed leaf abscission and increased break strength of the petiole AZ. These data clearly demonstrated the key role of polygalacturonases in the execution of organ abscission in tomato. Also using tomato as plant material and *TRV*-based vectors, it was shown the role of several auxin conjugate hydrolases and an auxin efflux facilitator in flower abscission: downregulation by VIGS of *SlILL1*, *SlILL5*, and *SlILL6* significantly reduced auxin concentration in pedicel AZs increasing flower abscission rate (Fu et al., 2019). Therefore, auxin conjugate hydrolases fine-tune the levels of auxin in tomato flower AZs, which is critical for abscission to occur. The silencing of *SlPIN1* accelerated flower abscission by increasing auxin accumulation in the ovary and decreasing the auxin content in the petiole AZ (Shi et al., 2017). Thus, it appears that *SlPIN1* mediated auxin source-sink transport and the establishment and maintenance of auxin maxima in the pedicel AZ to block tomato flower abscission.

VIGS has also been applied in the study of petal abscission. The role of an auxin/indole-3-acetic acid (AUX/IAA) transcription repressor and two ethylene response factors (ERFs) during petal abscission in hybrid tea rose (*Rosa hybrida*) was evidenced by VIGS using *TRV*-based vectors as well. Auxin perception and signal transduction involve the cooperative action of several components, including TRANSPORT INHIBITOR RESPONSE1/AUXIN SIGNALING (TIR1/AFB), Aux/IAA and auxin response factor (ARF) proteins (for a review, see Leyser, 2018). In presence of auxin, F-box TIR1/AFB proteins bind Aux/IAA proteins causing its degradation by the proteasome, which then releases repression of ARFs to trigger the expression of auxin responsive genes. Up-regulation of six *Aux/IAA* genes was detected in rose petal AZs during petal shedding (Gao et al., 2016). The silencing of one of these up-regulated

Aux/IAA genes, *RhIAA16*, by VIGS, accelerated petal abscission, suggesting that transcription repression by AUX/IAA proteins in petal AZs might be required to prevent premature abscission (Gao et al., 2016). It was also shown that the expression level of two ethylene response factors, *RhERF1* and *RhERF4*, was regulated by ethylene and auxin, respectively, in rose petal AZs during petal shedding (Gao et al., 2019). Treatment of rose flowers with ethylene reduced the expression of *RhERF1*, while the expression of *RhERF4* was significantly induced in petal AZs by auxin. VIGS silencing of both ERFs accelerate rose petal abscission, a process related to the reduction of pectic galactan in the rose petal AZ associated with the expression level of the β-GAL *RhBGLA1* (Gao et al., 2019).

The examples described above clearly show that VIGS is a simple and versatile functional genomics tool that can be successfully applied to characterize genes involved in organ abscission, including petals. In this section, a strategy based on *Citrus leaf blotch virus* (*CLBV*) VIGS vectors, previously developed in the laboratory of Dr. José Guerri at IVIA (Centro de Protección Vegetal y Biotecnología), was used to characterize the involvement of the pair of *NbenIDA1* homeologs and its potential receptor kinases, the pair of *NbenHAE* homeologs, that showed over-expression at the base of the corolla tube during corolla abscission (see section 4.9). *CLBV*-based viral vectors are able to either silence genes (*clbv3'* vector) or express proteins (*clbv3'pr* vector) both in citrus and *N. benthamiana* plants (Agüero et al., 2012, 2014; Velázquez et al., 2016; Gómez-Muñoz et al., 2017). The *CLVB* virus is not limited to the phloem and therefore reaches and accumulates in meristems and vegetative and reproductive organs (Agüero et al., 2013). In fact, green fluorescent protein (GFP) detection in corolla limb lobes of flowers from *N. benthamiana* plants inoculated with the construct *clbv3'pr*-GFP infective clone demonstrated that these vectors are also effective in reproductive tissues (Agüero et al., 2013). Constructs of *IDA*- and *HAE*-like genes into *CLBV*-based vectors of *N. benthamiana*, cloning of sequences used for silencing of endogenous genes or foreign protein expression, agroinoculation and cultivation of *N. benthamiana* plants, and determination of virus replication in inoculated plants, were performed in collaboration with members of the Dr. José Guerri's Research Group.

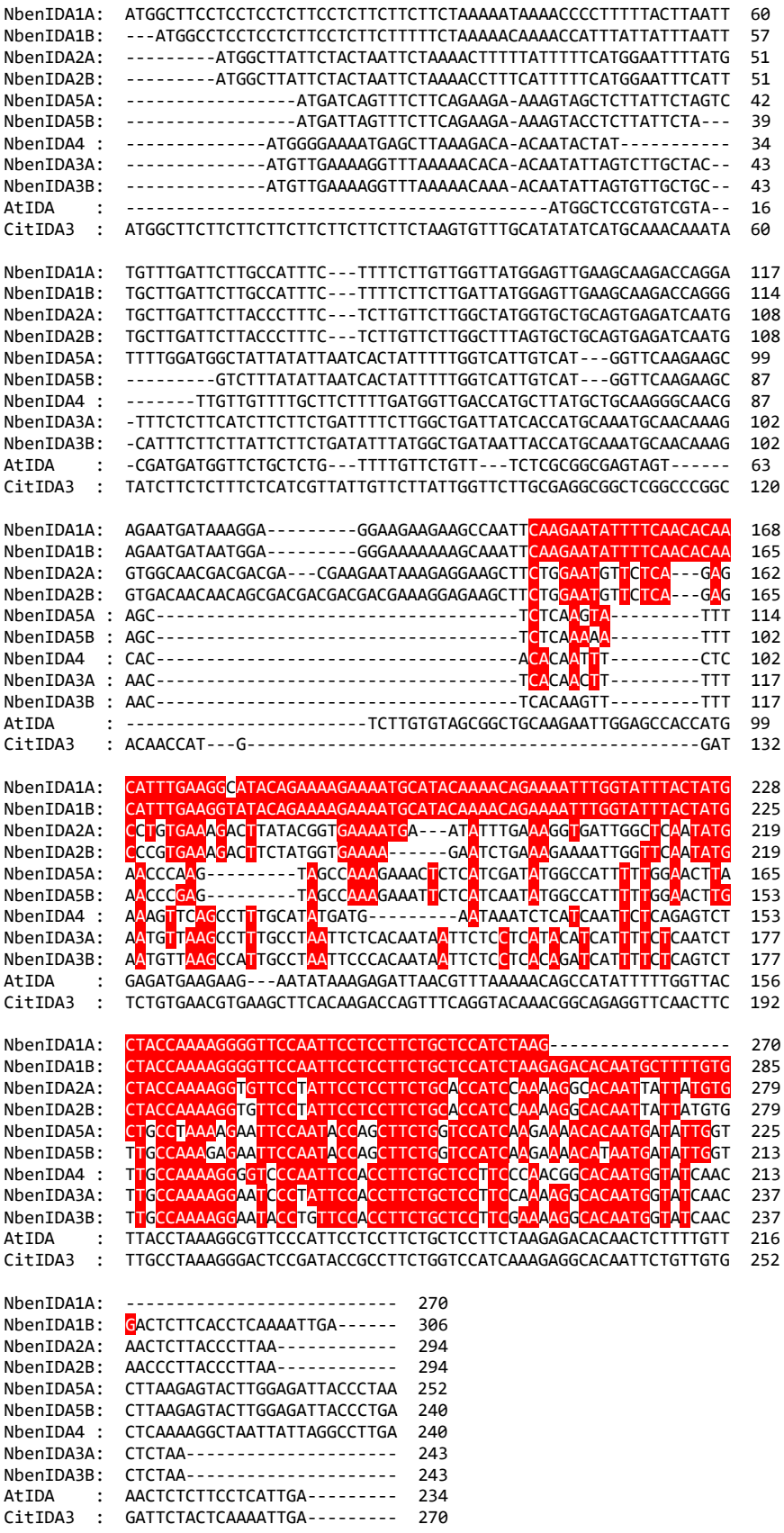
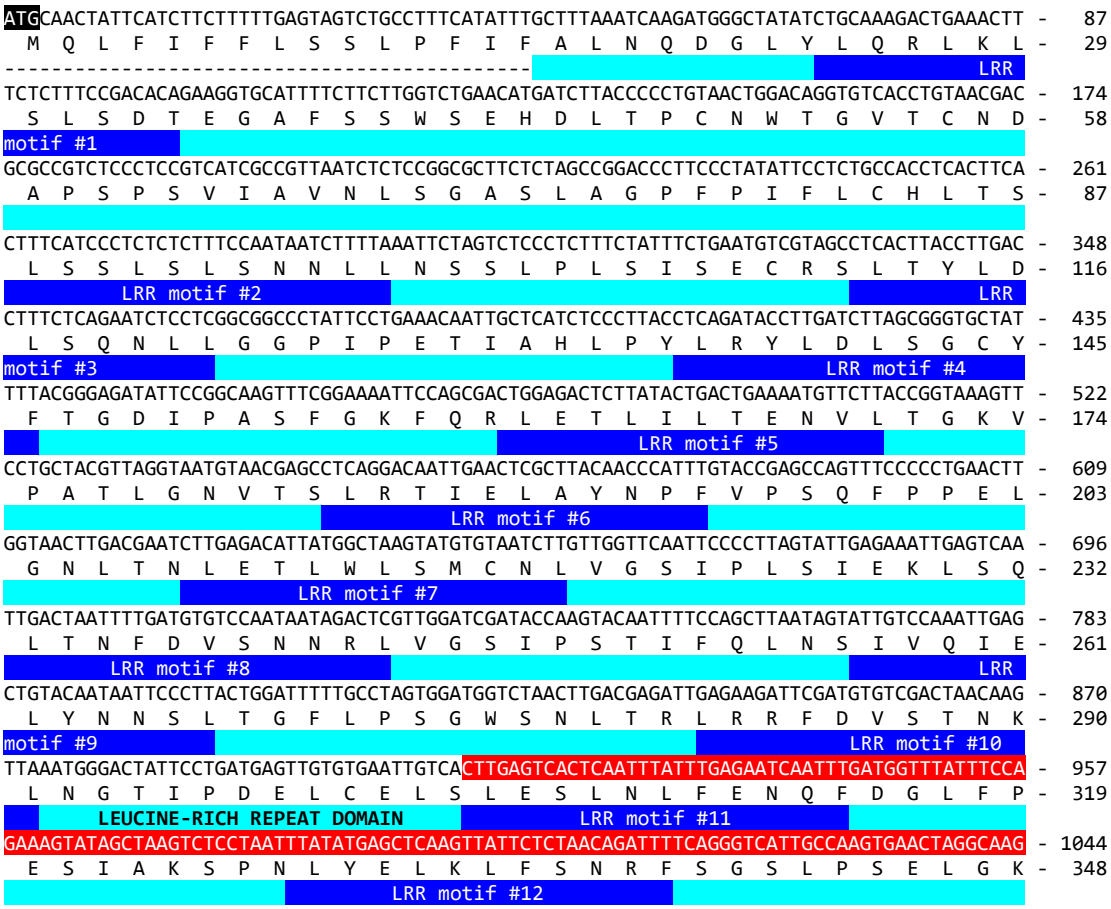


Figure 5.1. Multiple sequence alignment of all members of the *N benthamiana IDA*-like family, Arabidopsis *AtIDA* and citrus *CitIDA3* genes. The silencing trigger sequence selected in *NbenIDA1B* is shadowed in red, as well as the nucleotides conserved in the rest of the *N. benthamiana IDA*-like family members.

To generate the constructs of the *CLBV*-based vectors for the silencing of endogenous *N. benthamiana IDA*-like genes, we selected a 141-nt linear fragment of *NbenIDA1B* covering a portion of the variable region, the EPIP motif and a portion of the C terminus of the prepropeptide (Figure 5.1). Similarly, a 191-nt linear fragment of *NbenHAE.1* covering the LRR motifs #11, #12 and #13 of the Leucine-rich repeat domain of the receptor kinase (Figure 5.2) was amplified and used for the silencing of *HAE*-like genes. The selected silencing triggering sequence of *NbenIDA1B* had >99% identity with that of *NbenIDA1A,* suggesting that both *NbenIDA1* homeologs might be silenced with this construct (Figure 5.1). It has been experimentally established that silencing triggering sequences with at least one stretch of more than 21 nucleotides with 100% identity to the target gene sequence may be adequate to induce gene silencing in plants (Thomas et al., 2001; Senthil-Kumar et al., 2007). The fragment of *NbenHAE.1* showed >95% identity with that of *NbenHAE.2* and did not contain stretches higher than 21 nucleotides with 100% identity with other *HAE*-like receptor kinases of *N. bentamiana* (Figure 5.3). These conditions also suggest that both *NbenHAE* homeologs might be silenced. Both gene fragments were cloned into the *PmlI* restriction site of the *clbv3'* viral vector to obtain the constructs *clbv3'*-NbenIDA1 and *clbv3'*-NbenHAE (Figure 5.4).

To investigate the effect of the ectopic expression of *IDA*-like genes in *N. benthamiana* plants, we generated several other constructs in the *CLBV*-based expression vectors. Regions of *NbenIDA1A* gene from *N. benthamiana*, the *CitIDA3* gene from *Citrus clementina*, and the *AtIDA* gene from Arabidopsis (Figure 5.1) were cloned into the *clbv3'pr* vector to generate the *clbv3'pr*-NbenIDA1, *clbv3'pr*-CitIDA3 and *clbv3'pr*-AtIDA constructs, respectively (Figure 5.4).



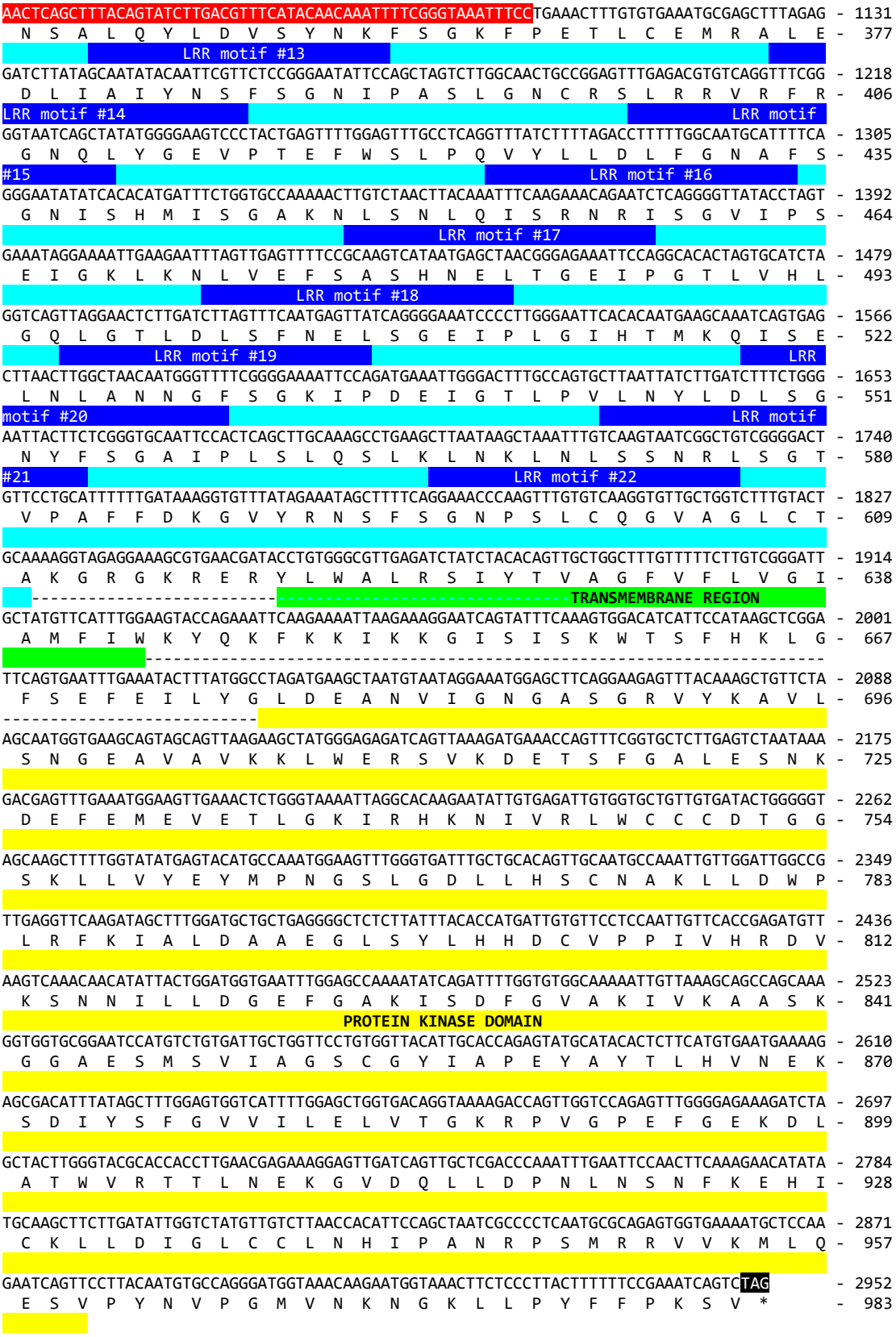


Figure 5.2. Nucleotide and deduced amino acid sequence of *NbenHAE.1*. Functional domains and motifs were annotated using InterProScan 5 (www.ebi.ac.uk/interpro/search/sequence/) and LRRsearch (www.lrrsearch.com). The sequence of the silencing triggering sequence is shadowed in red, the LRR motifs in dark blue, the transmembrane region in green and the protein kinase in yellow.

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NbenHAE.1 :   CCTAGTGGATGGTCTAACTTGACGAGATTGAGAAGATTCGATGTGTCGACTAACAAGTTA  873
NbenHAE.2 :   CCTAGTGGATGGTCTAACCTGACAAAATTGAGAAGATTCGATGTCTCAACTAACAAGTTT  813
NbenHSL2.1:   AACACG---TTTCCGGGACTTGTTTCTCTGTTCAGGTTTGACGCTTCTCAGAACAATCTC  891
NbenHSL2.2:   AACACG---TTTTCGGGACTTGTTTCTCTGTTCAGGTTTGATGCTTCTCAGAACAATCTC  891
NbenHSL1.1:   GTGAATGGGTGGTCGAAAATGACGGCGTTAAGGCGACTCGACGTGTCCATGAATCGGGTC  876
NbenHSL1.2:   GTGAGTGGGTGGTCGAAAATGACGGCGTTAAGGCGACTCGACGTGTCGATGAATCGGGTC  876

NbenHAE.1 :   AATGGGACTATTCCTGATGAGTTGTGTGAATTGTCACTTGAGTCACTCAATTTATTTGAG  933
NbenHAE.2 :   ACTGGTACTATTCCTGATGAGTTGTGTGATTTGTCACTTGAGTCACTCAACTTATTTGAG  873
NbenHSL2.1:   ACGGGAAAAATACCTGATAGCCTTGCCCGTTTGCCCTTAGTATCTTTGAATCTCAATGAT  951
NbenHSL2.2:   ACGGCAAAAATACCTGATAGCCTTGCCCGTTTGCCGCTAGTATCTTTGAATCTCAATGAT  951
NbenHSL1.1:   ACGGGTACGGTTCCTAGGGAGTTGTGTGAGTTGCCACTCGAGTCGCTGAATCTTTATGAG  936
NbenHSL1.2:   A-------------------------------------------------------------  877

NbenHAE.1 :   AATCAATTTGATGGTTTATTTCCAGAAAGTATAGCTAAGTCTCCTAATTTATATGAGCTC  993
NbenHAE.2 :   AATCAATTTGATGGTTTATTTCCAGAAAGTATAGCTAAGTCTCCTAATTTGTATGAGCTC  933
NbenHSL2.1:   AACAATTTAGAAGGCGAAATTCCAGAAAGTTTAGTTCTTAACCCGAATCTTACTCAGTTC  1011
NbenHSL2.2:   AACAATTTAGAAGGCGAAATTCCAGAAAGTTTATCTCTAAACCCGAATCTTACTCAGTTC  1011
NbenHSL1.1:   AACCAAATGTTCGGTGAATTGCCACAAGGCATTGCGAATTCGCCGAATTTGTATGAGTTG  996
NbenHSL1.2:   -------------------------------------------------------------  877

NbenHAE.1 :   AAGTTATTCTCTAACAGATTTTCAGGGTCATTGCCAAGTGAACTAGGCAAGAACTCAGCT  1053
NbenHAE.2 :   AAGTTATTCTCTAACAGATTTTCAGGGTCACTGCCTAGTGAACTAGGAAAGAACTCAGCT  993
NbenHSL2.1:   AAGCTCTTTAACAACAGATTTTCTGGTACTTTACCTCAAGATTTTGGTTTAAGTTCTGAT  1071
NbenHSL2.2:   AAGCTCTTTAACAACAGATTTTCAGGTACTTTACCTCAAGATTTTGGTTTAAGTTCAGAT  1071
NbenHSL1.1:   CGGCTCTTTCACAACCGTTTCAATGGGAGTTTACCTAATGATCTTGGGAAGAATTCGCCT  1056
NbenHSL1.2:   -------------------------------------------------------------  877

NbenHAE.1 :   TTACAGTATCTTGACGTTTCATACAACAAATTTTCGGGTAAATTTCCTGAAACTTTGTGT  1113
NbenHAE.2 :   TTACAGTATCTTGATGTTTCATACAACAAATTTTCTGGTAAAATTCCAGAAAGTCTGTGT  1053
NbenHSL2.1:   TTGGATGAGTTTGATGTCTCTGGCAATAATCTTGAAGGTTCTTTGCCGCCCAACTTATGT  1131
NbenHSL2.2:   TTGGATGAGTTTGATGTCTCTGGCAATAATCTTGAAGGTTCTTTGCCGCCCAACTTATGT  1131
NbenHSL1.1:   TTGTTGTGGATTGATGTGTCTGAGAATAAATTTTCCGGTGAAATTCCGGAAAATTTATGT  1116
NbenHSL1.2:   -------------------------------------------------------------  877
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Figure 5.3. Multiple sequence alignment of all members of the *N benthamiana HAE*-like family. The silencing triggering sequence selected in *NbenHAE.1* is shadowed in red as well as the nucleotides conserved in the rest of the *N. benthamiana HAE*-like family members.

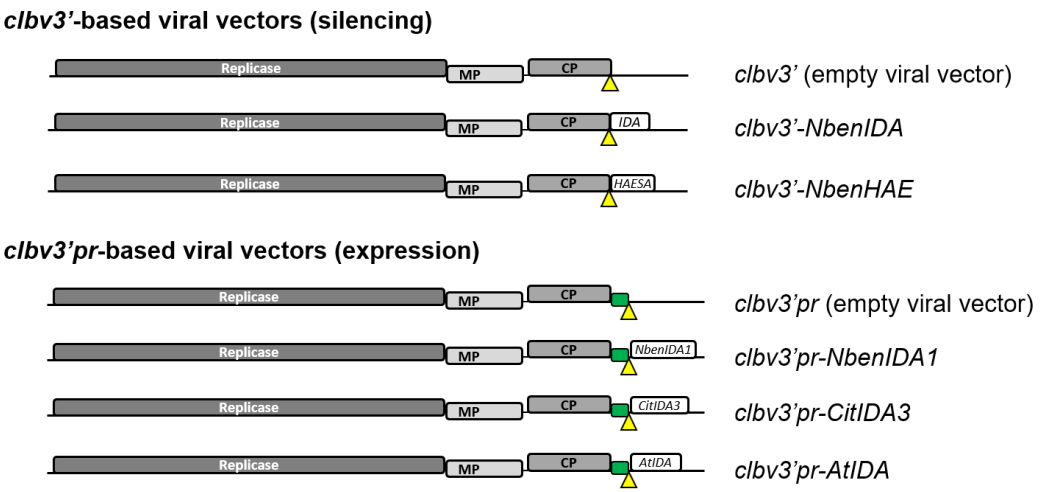

Figure 5.4. *CLBV*-based viral vectors and constructs used in the study. Green boxes and yellow triangles represent the duplicated capsid protein (CP) sgRNA promoter and the *PmlI* restriction site added for cloning, respectively.

Systemic spread of the infection was assessed by RT-PCR detection of the *CLBV* virions constructs in non-inoculated upper leaves of *N. benthamiana* plants, 20 days post inoculation. *CLBV* was detected in all plants infected with all constructs showed in Figure 5.4, indicating that the modified *CLBV* virions retained their capacity to systemically infect *N. benthamiana* plants (Figure 5.5).

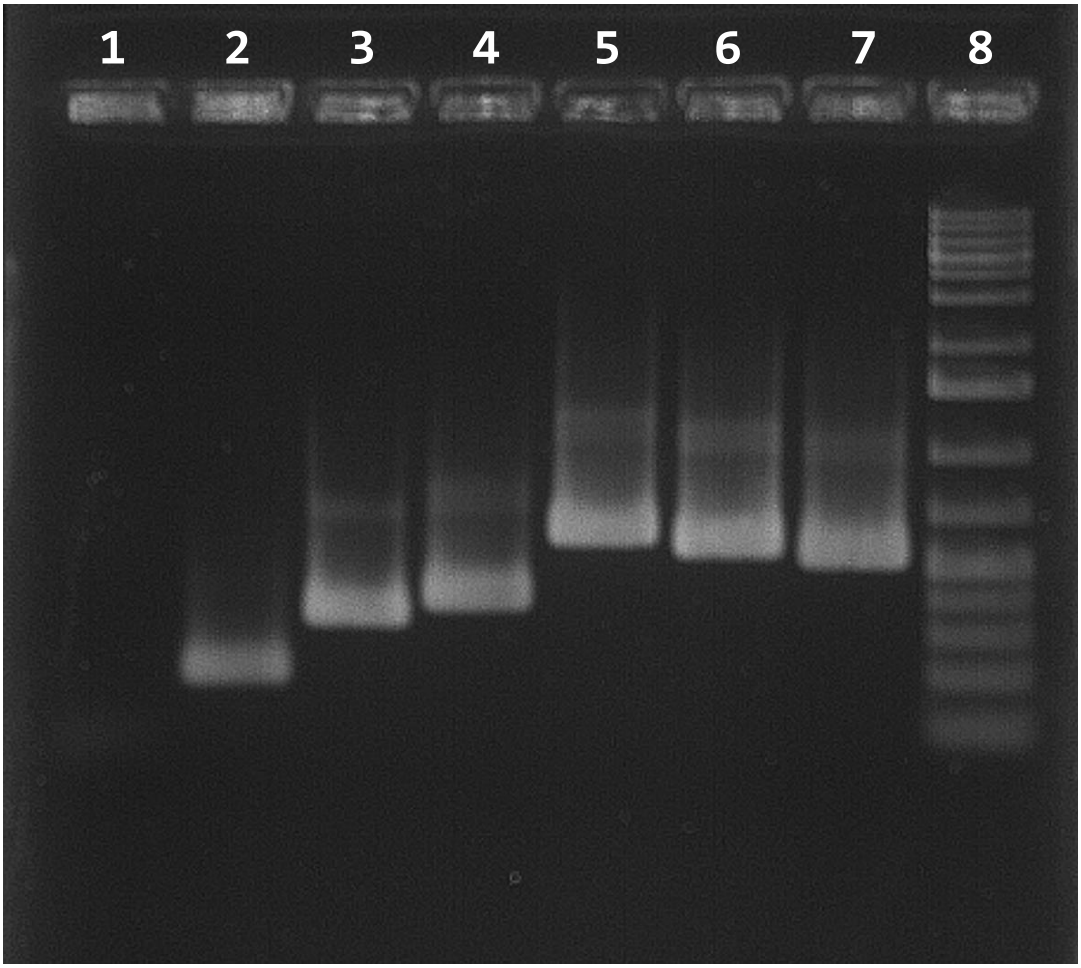

Figure 5.5. Reverse-transcriptase polymerase chain reaction analysis of total RNA from upper leaves of agroinoculated *N. benthamiana* plants 20 days post inoculation. Line 1: healthy, non-inoculated plant; line 2: *clbv3'*-control; line 3: *clbv3'*-NbenIDA; line 4: *clbv3'*-NbenHAE; line 5: *clbv3'pr*-NbenIDA1; line 6: *clbv3'pr*-CitIDA3; line 7: *clbv3'pr*-AtIDA; line 8: 1-Kb Plus molecular size ladder.

5.2. The inoculation of *clbv3'*-NbenIDA and *clbv3'*-NbenHAE constructs arrests corolla abscission

At the morphological level, the inoculation of *clbv3'*-NbenIDA and *clbv3'*-NbenHAE constructs did not produce any obvious effect on plant growth, either affected the rate of development or size of the major vegetative and reproductive organs of the inoculated plants (Figure 5.6). However, although plants inoculated with both constructs grew and developed normally just as controls, it was conspicuous that the bases of their flower corollas remained attached to the flower receptacles. This observation is rather relevant since in control plants the corolla bases eventually disappear, while the corolla tubes are then weakly attached to the apical end of the capsule (Figure 5.7).

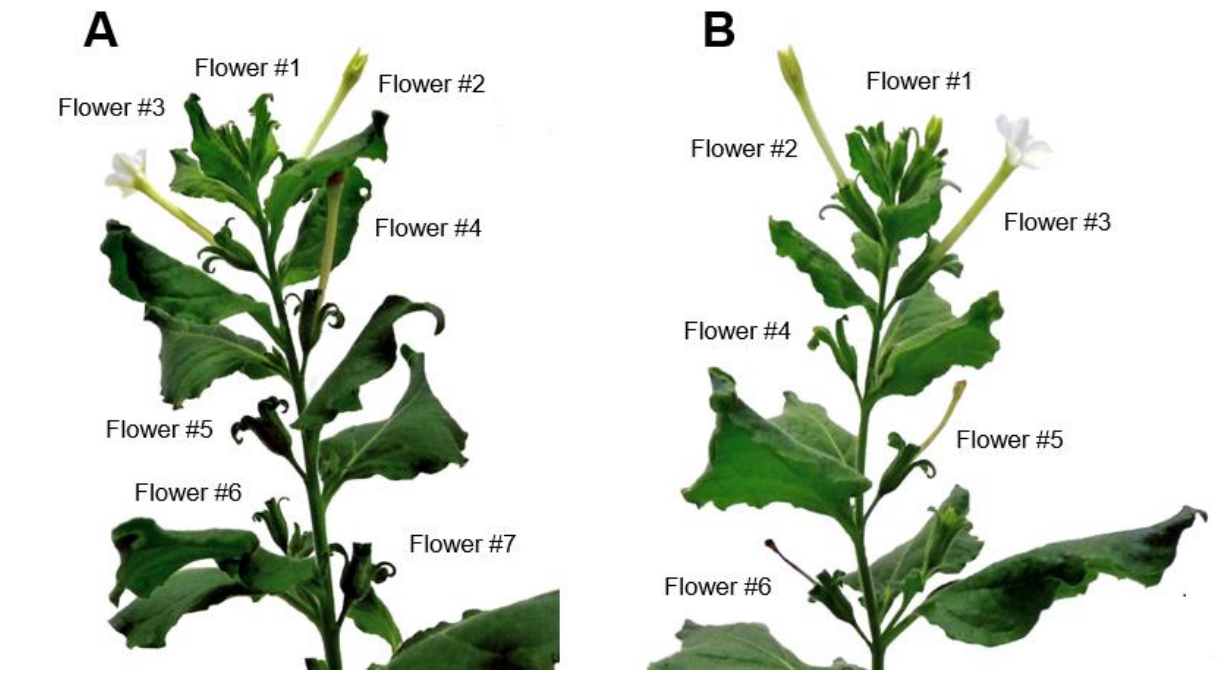

Figure 5.6. Morphological phenotypes of *N. benthamiana* plants, 4 weeks post inoculation of the empty *CLBV* vector, *clbv3'*-control, **(A)** and *clbv3'*-NbenIDA construct **(B)**.

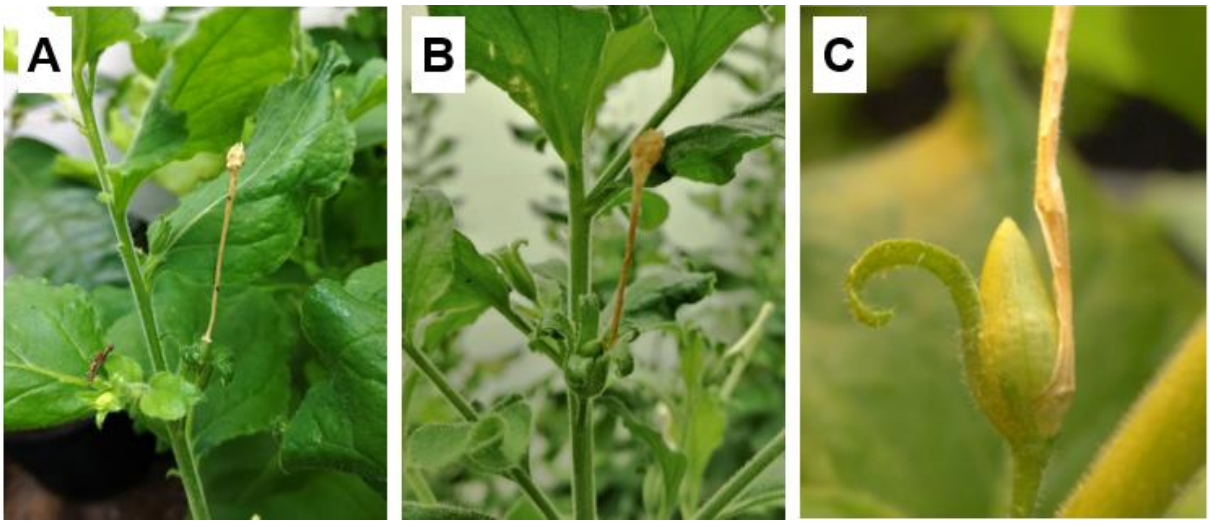

Figure 5.7. Attachment of necrotic corollas in control *clbv3'* vector and *clbv3'*-NbenIDA and *clbv3'*-NbenHAE constructs in *N. benthamiana* plants. **(A)** In plants inoculated with the *clbv3'* vector, the base of the necrotic corolla tubes has completely disappeared in advanced stages of flower development. In these plants, the necrotic corolla tubes are only weakly held by the pointed apical end of the capsule. **(B)** In plants inoculated with *clbv3'*-NbenIDA construct, necrotic corolla tubes remain attached to flowers. **(C)** A close-up of a flower from a plant inoculated with *clbv3'*-NbenHAE construct. Part of the sepals have been removed showing that the necrotic corolla tube is still attached to the receptacle.

Natural shedding of *N. benthamiana* corollas takes place after stage 7 of flower development, as described in the previous section, coinciding with the completion of the senescence process of the corolla. Quantitation of the number of retained/abscised corollas in control plants, and plants inoculated with both *clbv3'*-NbenIDA and *clbv3'*-NbenHAE constructs, revealed that at

stage 7, both silenced plants retained a higher number of corollas attached to the flowers than control plants. Among the two silenced plants, the *clbv3'*-NbenIDA construct produced a slightly higher percentage of retention (Figure 5.8A). At this stage, approximately 50% of the corollas were detached in control plants, while in plants inoculated with *clbv3'*-NbenIDA and *clbv3'*-NbenHAE constructs, total abscission of the corollas was 10% and 18%, respectively.

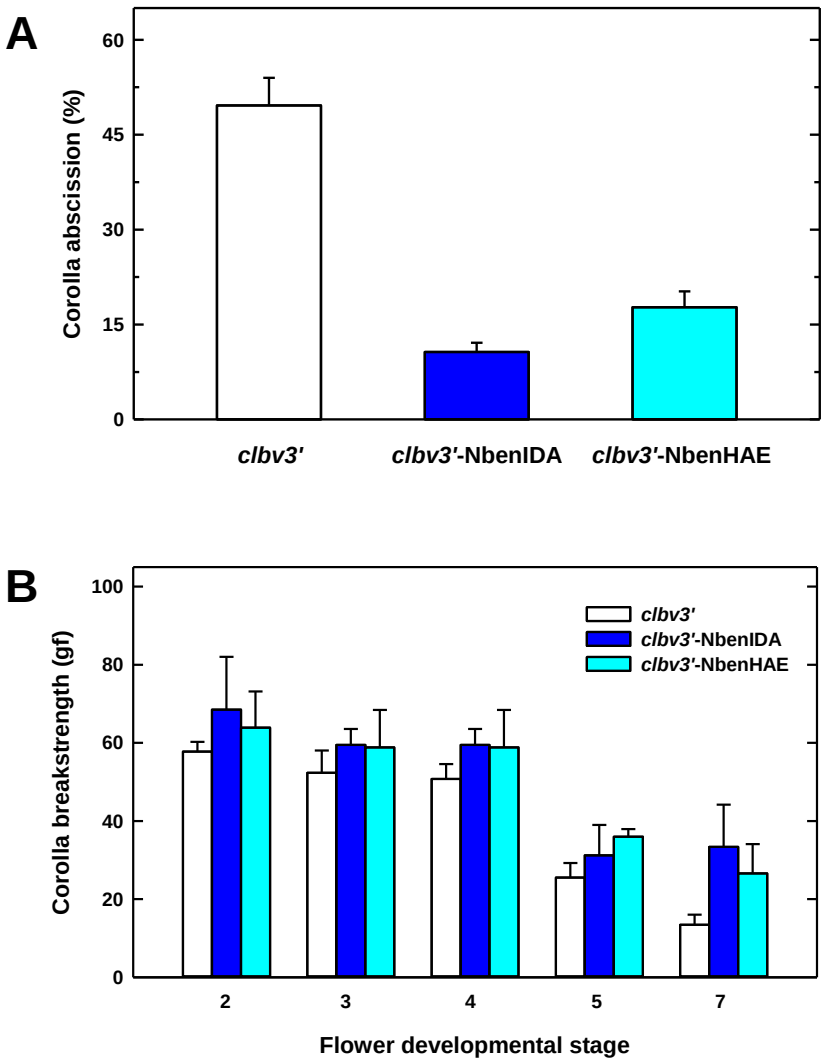

Figure 5.8. Corolla attachment in *N. benthamiana* plants inoculated with the empty *clbv3'* vector and the silencing *clbv3'*-NbenIDA and *clbv3'*-NbenHAE constructs. **(A)** Percentage of corollas shed in stage 7 of flower development. **(B)** Force required to remove the flower corolla (corolla breakstrength; cBS). All results are means of 4 silencing experiments involving 6 plants per inoculation (≥ 40 measurements at each flower developmental stage) ± standard error.

In order to determine the force required to remove flower corollas in *N. benthamiana* plants, we followed the approach originally developed in Arabidopsis to study petal abscission (Butenko et al., 2003): petal breakstrength (pBS) was measured by quantitating the force required to remove a petal from the receptacle of the flower. In Arabidopsis, pBS gradually falls to zero as the flower develops, due to cell wall loosening (Butenko et al., 2003). When pBS equals zero, petals are naturally shed and this occurs around floral position 8, counting flowers from top to bottom of the inflorescence.

In *N. benthamiana* plants, we measured the corolla breakstrength (cBS) using a dynamometer, and the force required to remove the corolla tubes of control and silenced plants was determined at different flower developmental stages (Figure 5.8B). Control plants exhibited a gradual decline of cBS values in flowers at stages 2 to 7 (Figure 5.8B). Both control and silenced plants required a similar amount of force to detach corollas in flowers between stages 2 to 4. At the end of the experiments, at flower stages 5 and 7, control plants required a smaller amount of force to detach the corollas in comparison with silenced plants. At stage 7, corolla detachment in control plants was reached with forces as weak as about 10 gf, while in the case of the corollas of plants inoculated with *clbv3'*-NbenIDA and *clbv3'*-NbenHAE constructs, higher strengths, about 30 and 40 gf, were required respectively.

cBS measurements in plants inoculated with *clbv3'*-NbenIDA1 and *clbv3'*-NbenHAE constructs remained stable during stages 5 to 7 (Figure 5.8B). This feature is clearly associated with the arrest of corolla abscission observed in silenced plants (Figure 5.6B, 5.7B/C, and 5.8A). In the introduction to this section, we provide much information suggesting that the *IDA*-like and *HAE*-like genes may function as an abscission regulating module in several species. However, this regulatory function has only been demonstrated in Arabidopsis so far. Hence, the arrest of corolla shedding observed in *N. benthamiana* plants inoculated with *clbv3'*-NbenIDA and *clbv3'*-NbenHAE constructs showed that the IDA-HAE/HSL2 module is certainly functional in the regulation of abscission and that it might be conserved in the angiosperms.

5.3. Anatomy of the base of the corolla tube in flowers from plants inoculated with the control *clbv3'* vector and the *clbv3'*-NbenIDA construct

To determine whether the observed differences in the force required to separate the corollas from the flowers between *N. benthamiana* plants inoculated with the control *clbv3'* vector and the *clbv3'*-NbenIDA construct, could be due to modifications on the corolla anatomy, we prepared and examined longitudinal semi-thin sections (about 1 µm thick) of flowers at the level of the junction of the corolla tube to the receptacle.

The microscopic inspection of wild-type flowers at stage 5 revealed the collapse of the parenchyma over a wide area at the base of the corolla tube, probably due to the action of cell wall hydrolytic enzymes (Figure 5.9). Therefore, this anatomical situation might explain the halving of the cBS values observed in wild-type flowers at this developmental stage (see Figure 5.8B). In addition, the walls of the adaxial and abaxial epidermis showed no signs of structural damage suggesting that they should be protected from hydrolytic enzymes. A closer look at the walls of the epidermis cells highlighted a bright blue coloration different from those of the parenchyma cells still remaining in the tissue. Sections were stained with Toluidine blue, a cationic dye that binds to negatively charged groups (O'Brien et al., 1964). This dye is blue in an aqueous solution, but different colors are generated when binding with different anionic groups in the cell. A greenish blue or bright blue color is generated when it binds with aromatic substances such as lignin and tannins, suggesting that these substances might be deposited in or interact with the walls of epidermis cells at the base of the corolla tube. Serafini-Fracassini and co-workers (2002) reported that corolla senescence in cultivated tobacco flowers begins at a transition stage between open flower (stage 4) and when the loss of corolla turgidity is evident, a stage that is generally accompanied by the occurrence of a brown ring at the base

of the corolla tube (stage 5). At this developmental stage, the walls of the epidermis cells were remarkably auto-fluorescent at the base of the corolla tube. Since lignin, one of the most important auto-fluorescent molecules found in plants (Donaldson, 2020), is deposited in plant cell walls during senescence, it is possible that the resistance to hydrolysis of the walls of the epidermis cells at the base of the corolla tube of *N. benthamiana* flowers might be related to lignin deposition.

This putative role of protection of the lignin deposition may be linked with evidence showing that a lignin-free zone in the pedicel is crucial to seed shattering in rice (Yoon et al., 2014). In addition, the deposition of a honeycomb structure of lignin in the walls of cells surrounding Arabidopsis floral organ AZs appears to act as a mechanical brace to specifically localize cell wall dissolution in this tissue (Lee et al., 2018).

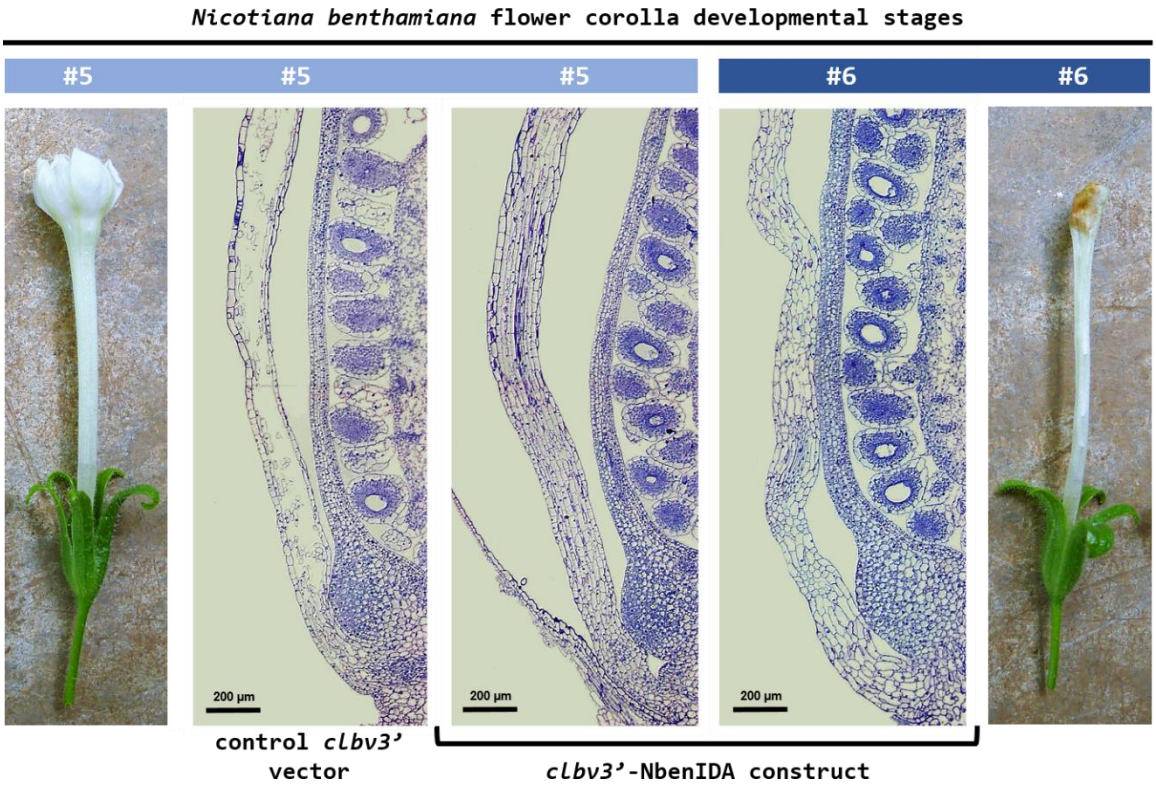

Figure 5.9. Anatomical comparisons at the base of the corolla tube between flowers of *N. benthamiana* plants inoculated with the control *clbv3'* vector and the *clbv3'*-NbenIDA construct.

The anatomical structure at the base of the corolla tube of flowers from plants inoculated with the *clbv3'*-NbenIDA construct was completely different from that observed in wild-type flowers. Cell wall breakdown observed at floral development stage 5 in the parenchyma tissue of wild-type corollas was completely arrested in flowers from plants inoculated with the *clbv3'*-NbenIDA construct (Figure 5.9). Parenchyma tissue cells retained cellular integrity in the base of the corolla tube at floral development stage 6 despite the wavy shape of the corolla. Corolla senescence was characterized by a gradual loss of turgor (see Figure 4.8C) and inoculation of the silencing construct does not appear to modify this process. The enlargement of the capsule contributes to the disintegration of the base of the senescent corolla tube, and therefore, to its detachment from the flower receptacle. The force with which the corolla withstands the enlargement of the capsule must apparently be related both to the maintenance of the

anatomical structure and to the loss of cell wall elasticity and cell turgor. Thus, the difference in cBS observed between wild-type corollas and those from silenced plants (see Figure 5.8B) might only be associated with the maintenance of the anatomical structure at the base of the corolla tube.

Wu and co-workers (2012) described the formation of an AZ at the base of the corolla tube in cultivated tobacco flowers and the anatomical changes that this organ undergone during the abscission process. According to this work, the corolla AZ at the open flower stage was characterized by the formation of several layers of parenchyma and epidermal cells shorter than the adjacent ones. Subsequently, when corolla senescence began, the middle lamella of the AZ cells dissolved, and the corolla was detached from the receptacle afterwards. In *NtBOP2* antisense plants, however, the parenchyma and epidermis cells were elongated at the base of the corolla tube but showed neither AZ formation nor tissue dissolution. This description of the anatomical changes at the base of the corolla tube in cultivated tobacco flowers appears to suggest that the corolla abscission process might be different from that of *N. benthamiana,* that apparently involves further dissolution of parenchyma tissue and intact epidermal cells.

5.4. Knockdown of target genes at the base of the corolla tube through inoculation with the *clbv3'*-NbenIDA and *clbv3'*-NbenHAE constructs

Inoculation of *clbv3'*-NbenIDA and *clbv3'*-NbenHAE silencing constructs to *N. benthamiana* plants successfully prevented flower corolla abscission by hindering parenchyma tissue breakdown at the base of corolla tubes (see Figures 5.7 and 5.9). Next generation sequencing was used to identify unequivocally the targets of *N. benthamiana IDA*-like and *HAE*-like gene families involved in abscission.

Three cDNA libraries (CLBV, IDAsil, and HAEsil) of *N. benthamina* corolla bases from flowers at developmental stage 4 collected from plants inoculated, respectively, with the empty *clbv3'* vector and the silencing constructs *clbv3'*-NibenIDA and *clbv3'*-NibenHAE, were prepared for Illumina Paired-End sequencing. After trimming and removing the adaptors, contamination and low-quality sequences, the Illumina sequencing generated 73,524,436 good sequence reads that were mapped to the transcriptome and genome sequences of *N. benthamiana* (Bombarely et al., 2012).

The Integrated Genome Viewer (IGV) is a high-performance desktop tool for visualization of short-read sequence alignments developed within the framework of the 1000 Genomes Project (Robinson et al., 2011; Thorvaldsdottir et al., 2013). By selecting a reference genome, in our case v1.0.1 of the *N. benthamiana* genome (Bombarely et al., 2012), multiple data sets can be mapped to genomic coordinates and therefore displayed simultaneously. The IGV browser allows in a single diagram called Sashimi plot (Katz et al., 2015), the information of read coverage along a gene with the visualization of transcript structure for multiple samples.

Since coding sequences (CDS) of *NbenIDA1A* and *NbenIDA1B* homeologs exhibited >92% nucleotide identity and the selected triggering sequence of NbenIDA1B had >99% identity with that of NbenIDA1A (see Figure 5.1), it could be predicted that both homeologs might be

silenced by *clbv3'*-NbenIDA VIGS construct. The BAM files for the three libraries mapped reads from the genomic regions of the *NbenIDA1* pair of homeologs (Figure 5.10). Sequencing reads of the CLBV and HAEsil libraries mapped the complete predicted sequence, without introns, of the *NbenIDA1* pair of homeologs. However, sequencing reads in the IDAsil library only mapped a fragment of the sequence of both homeologs that matched the silencing triggering sequence of the *clbv3'*-NbenIDA construct. The coverage range for the IDAsil library was very high (>3000 and >1000, respectively, for each homeolog), suggesting that the silencing construct was very active in the corolla base at flower developmental stage 4. Therefore, the silencing construct *clbv3'*-NbenIDA appeared to be very efficient, producing a strong knock-down effect on the expression of both *NbenIDA1A* and *NbenIDA1B* homeologs.

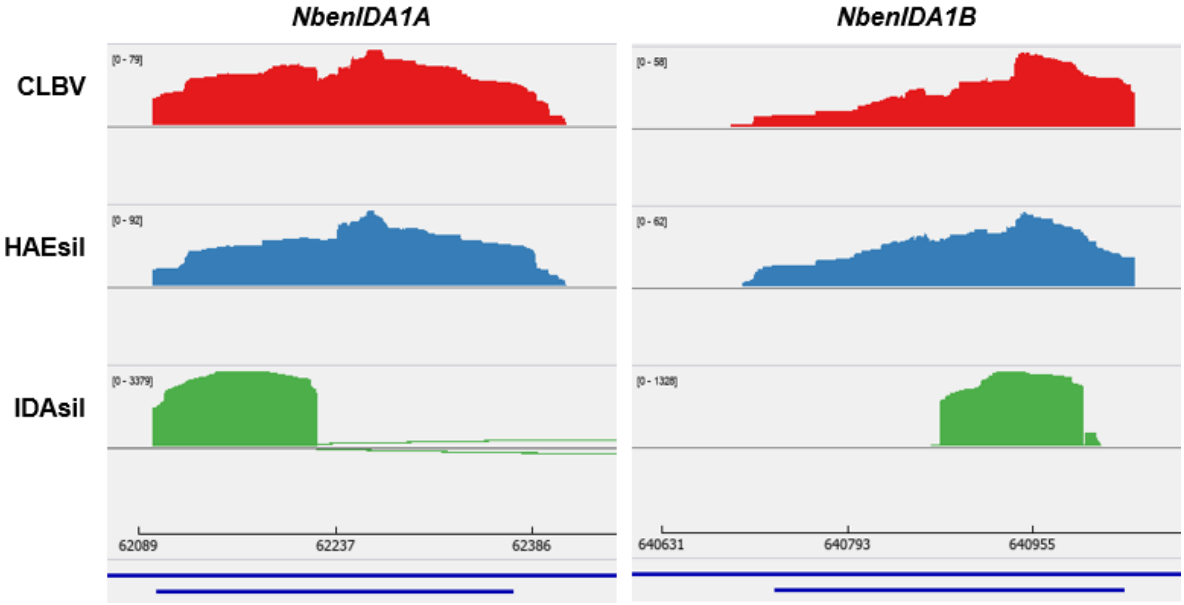

Figure 5.10. View of *NbenIDA1* pair of homeologs for the Integrated Genome Viewer (IGV). IGV-Sashimi plots showing the read coverage and transcript structures. The histograms represent the sum of the aligned sequencing reads along the genome. Red histograms represent coverage for the CLBV cDNA library (*clbv3'* control vector), blue for the HAEsil cDNA library (*clbv3'*-NbenHAE silencing construct) and green for the IDAsil cDNA library (*clbv3'*-NbenIDA silencing construct). Numbers in square brackets indicate coverage range. Below the histograms is shown in blue the transcript structure of each gene experimentally verified in this study.

The fragment of *NbenHAE.1* selected as silencing triggering sequence showed >95% identity with that of *NbenHAE.2* and contained stretches higher than 21 nucleotides with 100% identity in the first half of the sequence (see Figure 5.3). Therefore, it would be possible that both *NbenHAE* homeologs might be silenced. Sequencing reads of the CLBV and IDAEsil libraries mapped the complete predicted sequence of *NbenHAE1*, but those in the HAEsil library only mapped a fragment of the sequence that matched the silencing triggering sequence of the *clbv3'*-NbenHAE construct (Figure B). The coverage range for the HAEsil library was very high (almost 27000), suggesting that, as in the case of the other silencing construct, *clbv3'*-NbenHAE appeared to be very active for *NbenHAE.1* in the corolla base at flower developmental stage 4. However, sequencing reads of all three samples mapped the complete predicted sequence of *NbenHAE.2* even though the silencing triggering sequence showed >95% identity (see Figure 5.3). Therefore, the silencing construct *clbv3'*-NbenHAE appeared

to be very efficient producing only a strong knock-down effect on the expression of *NbenHAE.1*, but no effect on *NbenHAE.2*.

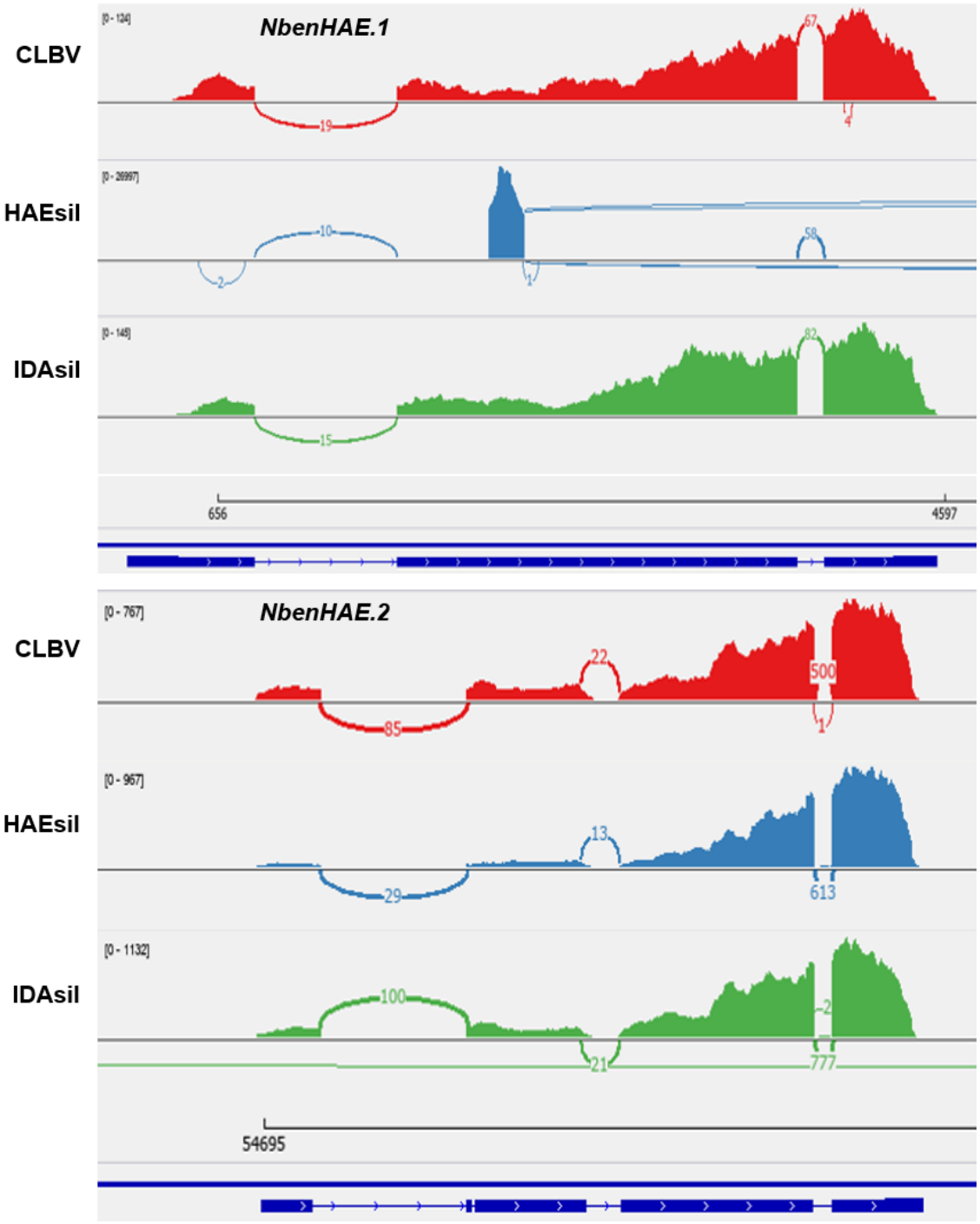

Figure 5.11. View of *NbenHAE* pair of homeologs for the Integrated Genome Viewer (IGV). IGV-Sashimi plots showing the read coverage and transcript structures. The histograms represent the sum of the aligned sequencing reads along the genome. Red histograms represent coverage for the CLBV cDNA library (*clbv3'* control vector), blue for the HAEsil cDNA library (*clbv3'*-NbenHAE silencing construct) and green for the IDAsil cDNA library (*clbv3'*-NbenIDA silencing construct). Numbers in square brackets indicate coverage range. Junction reads are plotted as arcs, and the number of reads aligned to the junction spanning the exons connected by the arc is indicated. Below the histograms is shown in blue the transcript structure of each gene experimentally verified in this study.

5.5. Overexpression of *NbenIDA1A* decreases plant growth and accelerates corolla senescence and abscission

A *CLBV*-based expression vector (*clbv3'pr*) containing an additional sgRNA promoter for stable and high-level expression (Agüero et al., 2012) was used to study the effect of increased transcript levels of the endogenous *NbenIDA1A* gene on *N. benthamiana* plants. This vector was also utilized to express foreign *IDA*-like genes from Arabidopsis (*AtIDA*) and citrus (*CitIDA3*). It is important to note that *AtIDA* was the gene that gave name to the Arabidopsis gene family and has a key role in the regulation of cell separation in different physiological processes including organ abscission (for a recent review, see Shi et al., 2019). On the other hand, the gene of the *IDA*-like family of citrus *CitIDA3*, is being expressed in the AZs of different citrus organs during abscission, when heterologously overexpressed in Arabidopsis is able to rescue the abscission phenotype of the *ida2* mutant (Estornell et al., 2015).

Regarding plants inoculated with the *clbv3'pr*-NbenIDA1 construct, the expression level of *NbenIDA1A* in the corolla base of stage 4 flowers was more than six times higher than that in wild-type flowers (Figure 5.12). Therefore, the phenotype of plants inoculated with the *CLBV* expression vector *clbv3'pr*-NbenIDA1 should be related to the over-accumulation of *NbenIDA1A* transcripts.

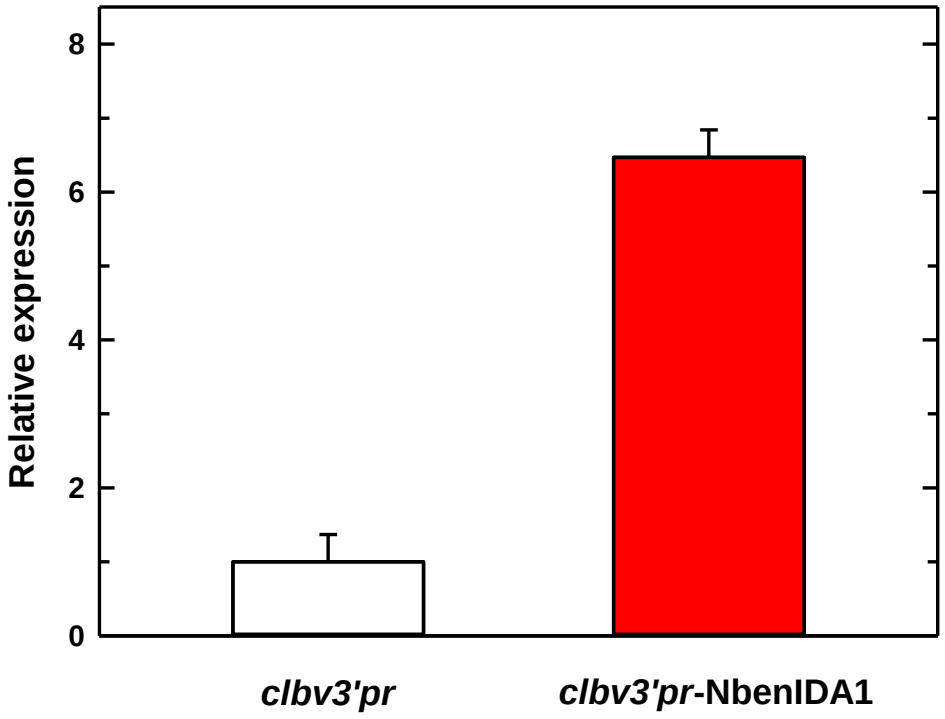

Figure 5.12. Relative expression levels of *NbenIDA1A* in the corolla base of stage 4 flowers in *N. benthamiana* plants inoculated with the control *clbv3'pr* vector and the *CLBV* expression construct *clbv3'pr*-NbenIDA1. Relative expression levels correspond to mean values of four samples from six independent agroinoculated plants.

Plants inoculated with *clbv3´pr*-CitIDA3 and *clbv3´pr*-AtIDA vectors were basically undistinguishable from those inoculated with *clbv3´pr*-control since their vegetative growth was standard (Figure 5.13), and their flowers senesced and were shed from the flower receptacles in normal positions (Figure 5.14). However, plants inoculated with *clbv3´pr*-NbenIDA1 vector exhibited three notorious phenotypical changes as related to the other kinds of plants:

a) *Clbv3´pr*-NbenIDA1 mature plants showed a dwarf phenotype that affected the whole plant architecture, including leaf area and size, internode and corolla length, flower size and shoot stature (Figures 5.13, 5.14 and 5.15). As an example of the effect of the over-expression of the endogenous *NbenIDA1A* gene, the length of the flower corollas was measured and compared with those of the plants inoculated with the empty expression *CLBV* vector (*clbv3'pr*-control) and with *clbv3'pro*-CitIDA3 (Figure 5.15). It was evident that the length of the flower corollas corresponding to the plants inoculated with the expression vector *clbv3'pr*-NbenIDA1 was shorter than that of the wild-type plants and also of the plants inoculated with the expression vector *clbv3'pr*-CitIDA3.

b) Corollas senesced prematurely, reaching full senescence just after stage 2 of flower development; these flowers directly developed into necrotic-stage 7 flowers. Plants inoculated with *clbv3´pr*-NbenIDA1 did not exhibit flowers at intermediate stages (3 to 6).

c) Corolla abscission of flowers from plants inoculated with the expression vector *clbv3'pr*-NbenIDA1 was also accelerated (Figure 5.16). Thus, enhanced levels of *NbenIDA1A* resulted in a dramatic decrease of the force required to remove the corollas, with values around 3 gf. It should be noted that this effect was precisely the opposite of that observed in *NbenIDA1*-silenced plants, as showed in section 5.3, adding further evidence to the notion that the IDA-HAE/HSL2 signaling module regulates corolla abscission in *N. benthamiana.*

Figure 5.13. Virus induced gene expression of endogenous *NbenIDA1A* and *IDA*-like genes from citrus (*CitIDA3*) and Arabidopsis (*AtIDA*) in *N. benthamiana* plants. Stunting of plants inoculated with *clbv3'pr*-NbenIDA1 in comparison with plants inoculated with the empty viral vector (*clbv3'pr*-control) and with *clbv3'pr*-CitIDA3 and *clbv3'pr*-AtIDA.

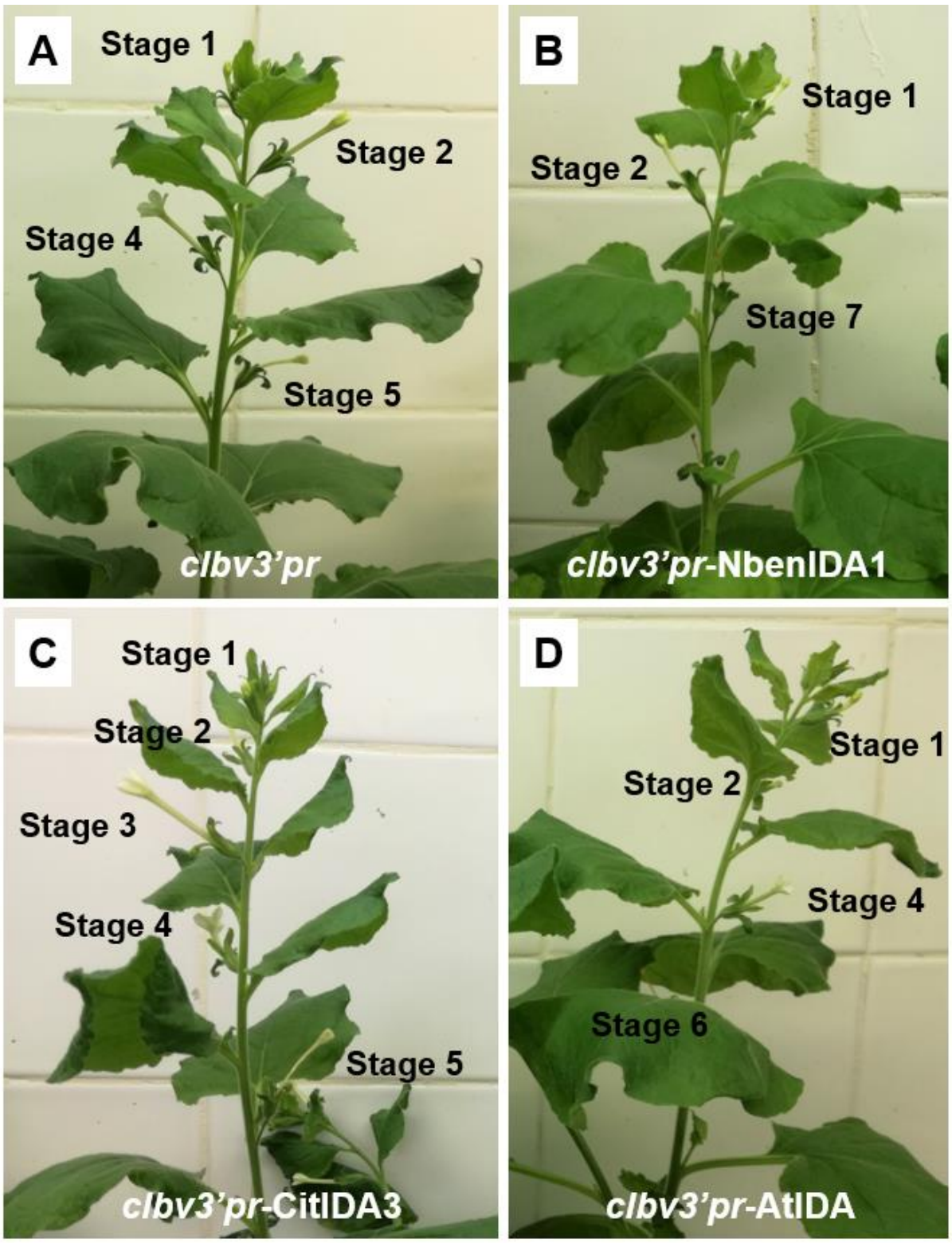

Figure 5.14. Close-up of the apical portions of *N. benthamiana* plants inoculated with the empty expression *CLBV* vector, *clbv3'pr*, **(A)** and with *clbv3'pr*-NbenIDA1 **(B)**, *clbv3'pr*-CitIDA3 **(C)**, and *clbv3'pr*-AtIDA **(D)** constructs. Figures A to D show the flower development stages of the plants inoculated with each of the *CLBV* expression vectors. It is interesting to note that while in Figures A, C, and D the series of flower developmental stages ranges from 1 to 5 or 6, in Figure B, only flowers at stages 1, 2 and 7 remain, while flowers at stages 3 to 6 were missing. These flowers are apparently smaller and carry shorter corollas.

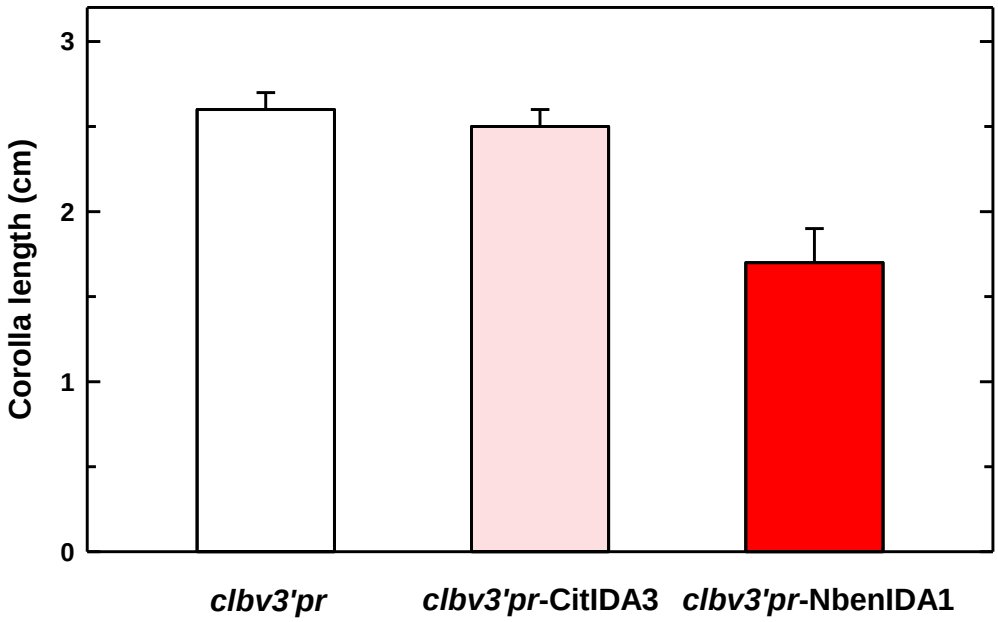

Figure 5.15. Corolla length (cm) of *N. benthamiana* flowers at stage 2 from plants inoculated, respectively, with the empty expression vector (*clbv3'pr*) and vectors expressing the foreign citrus *CitIDA3* gene (*clbv3'pr*-CitIDA3) and the endogenous *NbenIDA1A* gene (*clbv3'pr*-NbenIDA1). Results are the mean of 15 measurements per sample. Error bars are standard deviations from the mean.

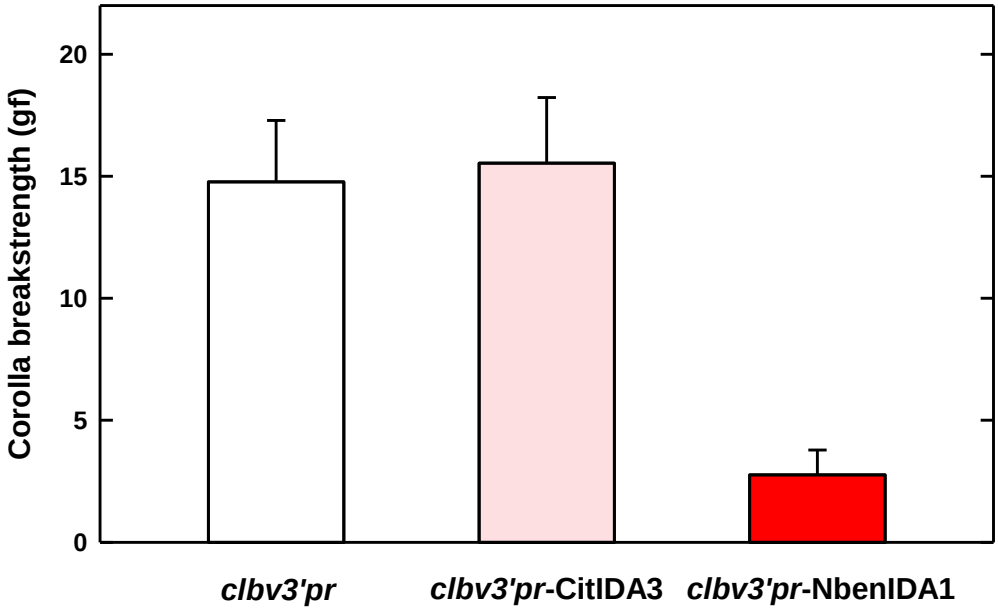

Figure 5.16. Corolla breakstrength (cBS) needed to tear out the flower corolla at flower developmental stage 7 in plants inoculated, respectively, with the empty expression vector (*clbv3'pr*) and constructs expressing the foreign citrus *CitIDA3* gene (*clbv3'pr*-CitIDA3) and the endogenous *NbenIDA1A* gene (*clbv3'pr*-NbenIDA1). Results are the mean of 15 measurements per sample. Error bars are standard deviations from the mean.

Taken together, these results indicate that overexpression of the endogenous *NbenIDA1A* in *N. benthamiana* plants affected both vegetative and reproductive development. *NbenIDA1A*-overexpressing plants showed a dwarf phenotype affecting practically all shoot organs. Reproductive development was also affected in different ways, since the flowers developed rapidly and, in many cases, did not set fruits. In addition, floral senescence and corolla abscission was markedly accelerated. Most of these phenotypic alterations resemble those produced by the ectopic overexpression of the endogenous *AtIDA* and the foreign citrus gene *CitIDA3* in Arabidopsis (Stenvik et al., 2006; Estornell et al., 2015). Additionally, the heterologous expression of litchi *LcIDL1* in Arabidopsis also produced early floral organ abscission, although no other features associated with the vegetative or reproductive development of transgenic plants were reported (Ying et al., 2016).

As mentioned above, Arabidopsis *AtIDA* and citrus *CitIDA3* regulate organ abscission in Arabidopsis (Butenko et al., 2003; Estornell et al., 2015). Interestingly, heterologous overexpression of *CitIDA3* in Arabidopsis produced a phenotype of plant growth reduction, acceleration of organ senescence and abscission similar to that observed after *AtIDA* overexpression (Stenvik et al., 2006; Estornell et al., 2015). However, the heterologous ectopic overexpression of *CitIDA3* and *AtIDA* in *N. benthamiana* did not alter the phenotype (see Figures 5.13 and 5.14). The standard phenotype that these plants exhibit might be associated with the proteolytic processing machinery required to mature *IDA*-like propeptides in *N. benthamiana*. Proteolytic cleavage is necessary to produce a mature IDA peptide of optimal length for receptor binding. Specific subtilases (AtSBT5.2, AtSBT4.12 and AtSBT4.13) are involved in the C-terminal processing for peptide maturation cleaving off the AtIDA propeptide, two amino acids upstream of the PIP domain (Schardon et al., 2016). These AtIDA-specific Arabidopsis subtilases must contain active sites suited to bind targets with particular amino acid series. In fact, the five amino acids upstream of the PIP domain are highly similar between AtIDA and CitIDA propeptides. The amino acids series in both propeptides are constituted by an amino acid with non-polar aromatic side-chain (tyrosine [Y] in AtIDA and phenylalanine [F] in CitIDA3), an identical core of four amino acids (leucine [L]-proline [P]-lysine [K]-glycine [G]), but an amino acid with non-polar aliphatic side-chain, valine (V), in AtIDA and an amino acid with polar neutral side-chain, threonine (T), in CitIDA3 (Figure 5.17). Actually, the highly similar chemical nature of these two series of amino acids might be related to the fact that heterologous expression of *CitIDA3* in Arabidopsis was effective both in phenocopying the effect of endogenous *AtIDA* overexpression and in rescuing the abscission deficiency of the *ida2* mutant (Estornell et al., 2015). In *N. benthamiana*, the amino acids with non-polar aromatic side chains are substituted in the pair of NbenIDA1 propeptides by methionine (M), an amino acid with non-polar aliphatic side chain (Figure 5.17). Thus, IDA propeptides containing amino acids with non-polar aromatic side chains may not successfully bind to active sites of *N. benthamiana* subtilases involved in C-terminal processing. As a result, the enzymatic cleavage of CitIDA3 and AtIDA propeptides may not be effective and, therefore, the wild-type phenotype is not modified. The feasibility of this scenario will have to be experimentally tested.

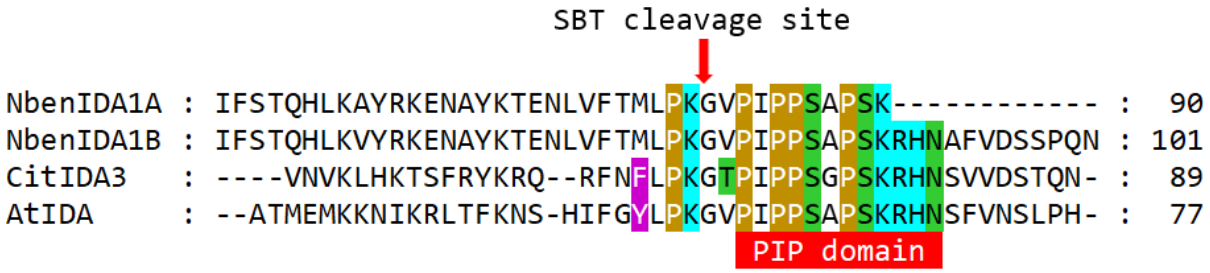

Figure 5.17. Multiple sequence alignment of the C terminal portion of both *N. benthamiana* NbenIDA1, citrus CitIDA3 and Arabidopsis AtIDA propeptides. Chemical nature of the amino acid residues upstream of and at the PIP domain: polar positive [X] and neutral [X] residues; non-polar aliphatic [X] and aromatic [X, and X] residues. SBT, subtilisin-like proteinase.

5.6. Conclusions

The VIGS approach used in this study to both silence the *NbenIDA1* pair of homeologs and its potential *NbenHAE* receptors and to overexpress *NbenIDA1A* yielded results compatible with a key role of these genes in the regulation of corolla abscission in *N. benthamiana*. The silencing effect of *clbv3'*-NbenIDA and *clbv3'*-NbenHAE at the base of corolla tubes is highly specific for target genes and efficiently suppressed the expression of the pair of *NbenIDA1* homeologs and the LRR-RLK *NbenHAE.1*. Inoculation of the *clbv3'pr*-NbenIDA1 construct produced an increase in the expression of *NbenIDA1A* at the corolla base. *NbenIDA1A* overexpression resulted in a reduction in plant growth and an acceleration of flower senescence and corolla abscission. These alterations in plant growth and development highly resembled those produced by the ectopic overexpression of the endogenous *AtIDA* and the foreign citrus gene *CitIDA3* in Arabidopsis (Stenvik et al., 2006; Estornell et al., 2015). On the other hand, the inoculation of *clbv3'*-NbenIDA and *clbv3'*-NbenHAE silencing constructs did not produce any obvious effect on plant growth but kept the senescent corolla tubes attached permanently to the flower receptacles. In wild-type plants, the onset of the cell separation process must take place very early, in stage 4 of flower development, specifically at the corolla base, and involved only parenchyma cells. The dissolution of pectins in the middle lamella and the disassembly of the primary cell walls progressively extended to parenchymal layers further away from the starting point of cell separation. However, the epidermis at the corolla base remained intact, without showing any signs of cell wall dissolution and disassembly. Inoculation of the *clbv3'*-NbenIDA and *clbv3'*-NbenHAE silencing constructs completely blocked cell breakdown in the parenchyma layers located at the corolla base. Thus, although the constant growth of the fruit ripped the senescent tissue of the corolla from stage 7 of flower development, this lack of parenchyma dissolution caused the corollas to remain attached. Hence, the results obtained through the inoculation of constructs to silence and overexpress members of the IDA-HAE/HSL2 module of *N. benthamiana* indicate that the module is certainly functional in the regulation of abscission. Outside of Arabidopsis, this is the first example claiming that the abscission regulatory module IDA-HAE/HSL2 might be conserved in the angiosperms.

6
General discussion

Abscission is a cell separation process taking place in groups of functionally specialized cells located in specific layers, known as abscission zones (AZs). This physiological process allows the shedding of aerial organs and historically through to modern times has been a major focus of plant biological research (Addicott, 1982; Sexton and Roberts, 1982; Osborne and Morgan, 1989; Taylor and Whitelaw, 2001; Roberts et al., 2002; Lewis et al., 2006; Roberts and González-Carranza, 2007; Liljegren, 2012; Estornell et al., 2013; Nakano and Ito, 2013; Ito and Nakano, 2015; Patharkar and Walker, 2016, 2018, 2019; Tranbarger and Tadeo, 2020). Abscission is also a fundamental process in plant biology that accounts for a highly beneficial evolutionary adaptation for plants because it allows for discarding senescent or physiologically damaged organs and for highly efficient seed dispersal. However, from an agricultural point of view, abscission has a huge impact on yield, leading to high production losses. Therefore, the greater the knowledge about the control of the abscission process, the more efficient in economic terms will be the cultivation of species of agronomic interest.

Solanaceae is a large plant family containing economically important species belonging to the genera *Solanum*, *Capsicum* and *Nicotiana*. Some species such as tomato (*S. lycopersicum*), potato (*S. tuberosum*), eggplant (aubergine; *S. melongena*) and pepper (*C. annum*) are of great relevance as a human food source, while species of the genus *Nicotiana* have medical importance as a source of plant drugs. On the other hand, *Nicotiana benthamiana* is considered a relevant model organism for the study of plant-microbe interactions and also in plant molecular research and biotechnology (Goodin et al., 2008; Bally et al., 2018). In this family, only the process of tomato flower and fruit abscission had received attention until now and, in fact, Tucker and Wang (2013) identified the first members of the *IDA*-like family in this species.

In the present survey, the identification of the *IDA*-like and *HAE*-like gene families has been carried out taking advantage of the free availability of the diploid genome sequences of tomato, eggplant, pepper, *N. Sylvestris*, *N. tomentosiformis*, the allopolyploids *N. tabacum* and *N. benthamiana*, and the double haploid genome sequence of potato in the Solanaceae Genomic Network (SGN; https://solgenomics.net/). New and relevant information on *IDA*-like families in Solanaceae has been provided highlighting all the members of potato (*StubIDA4*), eggplant (*SmelIDA5*), pepper (*CaIDA4*) and *Nicotiana* spp, (*NsylIDA1*, *NtomIDA1*, *NtabIDA1A/B*, and *NbenIDA1A/B*) potentially involved in organ abscission (Table 4.1 and Figures 4.1 and 4.2). In addition, new members belonging to the *IDA*-like family of tomato, *SlIDA6-8*, have also been

identified. The bioinformatic computational analysis of the *cis*-acting regulatory elements in the 5'-UTR regions of the *IDA*-like family members of *N. benthamiana* showed *cis*-acting regulatory elements related to abscisic acid, methyl jasmonate, auxins and gibberellins but not ethylene, in addition to other response elements related to drought (Figure 4.3). Interestingly, the promoter sequences of the pair of *NbenIDA1* homeologs were highly similar. They shared the same hormonal response elements in similar positions, in addition to the same drought response element. The high degree of conservation in the 5'-UTR sequence of the pair of *NbenIDA1* homeologs suggested that they might have a highly relevant role in the regulation of cell separation processes and in the response to environmental conditions. The pair of *NbenIDA2* homeologs also contained a drought response element in their promoter regions. Members of the *HAE*-like gene family have also been identified in these solanaceous species including tomato (Table 4.2 and Figure 4.4). The amino acid residues Ser62, Pro64, Ser65 and Asn69 of AtIDA, essential in the interaction with the peptide binding pocket of AtHAE (Santiago et al., 2016), were all conserved in the PIP domains of the Solanaceae IDA-like prepropeptides that may potentially be involved in abscission (Figure 4.5). Moreover, the critical amino acid residues in the peptide binding pocket Glu226, Phe289 and Ser331 were conserved between AtHAE, AtHSL2 and the pairs of NbenHAE and NbenHSL2 receptor kinases (Figure 4.6) suggesting that might be functional in organ abscission.

The expression of all members of the *IDA*-like family of the allopoliploid *N. benthamiana* in different organs during plant growth and development and also in leaves and roots from plants subjected to water stress conditions was also analyzed. The literature on the *IDA*-like family contains several examples showing a link between the increase in the expression of potential orthologues of *AtIDA* in leaf, flower and fruit AZs of citrus (*CitIDA3*), litchi (*LcIDL1*), oil palm (*EgIDA5*), yellow lupin (*LlIDA*), soybean (*GmIDA2a*) and tomato (*SlycIDA1*) and organ abscission execution. However, the role of *IDA*-like family members in organ abscission has only been demonstrated in Arabidopsis (Butenko et al., 2003). Regarding the involvement of *IDA*-like genes in the control of organ abscission, it is interesting to note that the over-expression of *CitIDA3* and *LcIDA1* accelerated abscission in Arabidopsis wild-type plants and rescued the abscission phenotype of the *ida2* mutant of Arabidopsis, suggesting that these genes (and perhaps all those that were located in the subclade of the clade I shaded on pale green in Figure 4.2) are most likely involved in the regulation of organ abscission as well. The *N. benthamiana* homeologs *NibenIDA1A* and *NibenIDA1B,* which were located in the same clade as *AtIDA*, *AtIDL1* and *SlycIDA1,* increased their expression level at the base of the flower corollas during flower growth and development, resulting in corolla abscission (Figure 4.9). In addition to organ abscission, it has been reported that some members of the *IDA*-like family of Arabidopsis are induced by stress (*AtIDA*, *AtIDL1*, *AtIDL6* and *AtIDL7*; Vie et al., 2015, 2017). In *N. benthamiana*, the expression of two pairs of homeologs is induced by dehydration specifically in leaves (*NibenIDA1A/B*) and in roots (*NibenIDA2A/B*), which are located in the same clade as *AtIDA* and *AtIDL1* (Figure 4.10). That is, specific members of the *IDA*-like family of *N. benthamiana* were also induced by stress as reported in Arabidopsis. In addition to their involvement in abscission and response to stressful environmental conditions, *IDA* genes may also regulate plant growth. The highest expression level of most members of the *IDA*-like family was found in nodes and internodes (Figure 4.9B). A tight control of the expression of *IDA*-like genes must be required for normal plant growth as their ectopic over-expression leads to a reduction in plant height and organ size (Stenvik et al., 2008; Estornell et al., 2015; Ying et al., 2016).

It is widely known that *N. benthamiana* is one of the most commonly used model plant organisms to perform host-pathogen interaction studies due to its hypersensitivity to viruses and other pathogenic agents (Goodin et al., 2008). But in addition, it is also feasible to perform transient expression studies in *N. benthamiana* plants and apply virus-induced gene silencing (VIGS) methods (Bally et al., 2018). Therefore, the function of members of the *IDA*-like and *HAE*-like gene families of *N. benthamiana* potentially involved in organ abscission was addressed using this experimental approach.

A strategy based on *Citrus leaf blotch virus* (*CLBV*) VIGS vectors was used to characterize the involvement of the pair of *NbenIDA1* homeologs and its potential receptor kinase *NbenHAE.1* in cell wall dissolution at the base of the corolla tube in *N. benthamiana* flowers. To this end, silencing constructs were generated using specific nucleotide sequences of *NbenIDA1B* covering a portion of the variable region, the EPIP motif, and a portion of the C terminus of the prepropeptide (*clbv3'*-NbenIDA1 construct; Figure 5.1), as well as the LRR motifs #11, #12 and #13 of the LRR domain of *NbenHAE.1* (*clbv3'*-NbenHAE construct; Figure 5.2). To investigate the effect of the ectopic expression of *IDA*-like genes in *N. benthamiana* plants, several other constructs in the *CLBV*-based expression vectors using the coding sequences of *NbenIDA1A* from *N. benthamiana*, *CitIDA3* from *Citrus clementina*, and *AtIDA* from Arabidopsis (*clbv3'pr*-NbenIDA1, *clbv3'pr*-CitIDA3 and *clbv3'pr*-AtIDA constructs, respectively; Figure 5.4) were generated.

The inoculation of *clbv3'*-NbenIDA and *clbv3'*-NbenHAE constructs did not produce any obvious effect on plant growth, either affected the rate of development or size of the major vegetative and reproductive organs of the inoculated plants (Figure 5.6), but arrested corolla abscission (Figures 5.6 and 5.7). Flowers in plants inoculated with both silencing constructs retained a higher number of corollas attached to the flowers than control plants (Figure 5.8A), an observation related to a greater corolla breakstrength (cBS), the force required to remove corollas from the flower receptacles (Figure 5.8B). The arrest of corolla abscission was associated with the preservation of the parenchyma tissue at the base of the corolla tube that, in contrast, was virtually collapsed in normal corollas (Figure 5.9).

The inoculation of the *clbv3'pr*-NbenIDA1 construct increased the expression of *NbenIDA1A* at the base of the corolla tube of *N. benthamiana* flowers (Figure 5.12), negatively affecting the growth of the inoculated plants (Figure 5.13) and the timing of both corolla senescence and abscission (Figure 5.14). *Clbv3´pr*-NbenIDA1 mature plants showed a dwarf phenotype that affected the whole plant architecture, including leaf size, internode and corolla length, flower size and shoot stature (Figures 5.13, 5.14 and 5.15). In these plants, corollas senesced prematurely reaching full senescence just after stage 2 of flower development, and shortly thereafter rapidly developed necrotic spots, a condition generally observed in normal plants at stage 7. Plants inoculated with *clbv3´pr*-NbenIDA1, therefore, did not exhibit flowers at intermediate stages (Figure 5.14). Corolla abscission was accelerated in parallel to a dramatic decrease in cBS (Figure 5.16). However, the heterologous ectopic overexpression of *CitIDA3* and *AtIDA* in *N. benthamiana* did not alter the standard plant phenotype (Figures 5.11 and 5.12), albeit both genes were apparently actively expressed (Figure 5.5). The standard plant phenotype that these plants exhibited appears to be associated with the proteolytic processing machinery required to mature *IDA*-like propeptides in *N. benthamiana*. The cleavage site of the

subtilisin-like proteinases is located two amino acids upstream of the PIP domain (Figure 5.17). The five amino acids upstream of the PIP domain are highly similar between AtIDA and CitIDA propeptides with amino acids series in both propeptides constituted by an amino acid with non-polar aromatic side-chain (tyrosine [Y] in AtIDA and phenylalanine [F] in CitIDA3) and an identical core of four amino acids (leucine [L]-proline [P]-lysine [K]-glycine [G]). However, the amino acids with non-polar aromatic side chains were substituted in the pair of *NbenIDA1* propeptides by methionine (M), an amino acid with non-polar aliphatic side chain (Figure 5.16), which suggests that the *N. benthamiana* subtilisin-like proteinases may not be able to process both propeptides, thus remaining inactive to trigger the signaling response.

Since the first reports by Jinn and co-workers (2000) and Butenko and co-workers (2003) showing, respectively, the involvement of the LRR-RLK HAESA and the small signaling peptide IDA in floral organ abscission in Arabidopsis, a large body of experimental evidence supports the regulatory role of the signaling module IDA-HAE/HSL2 in organ abscission (see subsection 1.4). The identification of a large number of putative Arabidopsis IDA orthologs and its HAESA family receptors (Stø et al., 2015) and the abundant experimental results obtained during leaf, flower and fruit abscission in vegetative and woody fruit crops (for a recent review, see Tranbarger and Tadeo, 2020), strongly suggested that the abscission regulatory module IDA-HAE/HSL2 is conserved in angiosperms. This signaling module also regulated other cell separation processes in Arabidopsis such as lateral root emergence (Kumpf et al., 2013) and root cap sloughing (Shi et al., 2018), and has been shown to be functional in the emergence of soybean lateral roots (Liu et al., 2018). In here, it is demonstrated that the pair of *NbenIDA1* homeologs encoding small peptides of the *IDA*-like family and the receptor *NbenHAE.1* control cell wall dissolution in the adventitious AZ formed at the base of the corolla tube and, therefore, the abscission of the corolla in *N. benthamiana* flowers. Outside of Arabidopsis, this is the first example claiming that the abscission regulatory module IDA-HAE/HSL2 might be conserved in the angiosperms.

7
Conclusions

The major findings arising from the study of the *IDA*-like and *HAE*-like gene families in different species of the Solanaceae family are summarized below.

1. The *IDA*-like and *HAE*-like gene families of potato, eggplant, pepper and several species of *Nicotiana* have been identified *de novo*. In tomato, the *IDA*-like gene family has been extended, and the members of its *HAE*-like gene family, identified.

2. All members of the *IDA*-like gene families of potato (*StubIDA4*), eggplant (*SmelIDA5*), pepper (*CaIDA4*) and *Nicotiana* spp, (*NsylIDA1*, *NtomIDA1*, *NtabIDA1A/B*, and *NbenIDA1A/B*) potentially involved in organ abscission have been revealed.

3. The expression level of most members of the *IDA*-like family of *N. benthamiana* was high in nodes and internodes, suggesting a potential involvement in stem growth. *NbenIDA2B* and *NbenIDA4* showed the highest expression level and its promoter regions contained gibberellin response elements, a hormone with a fundamental role in plant growth.

4. The pair of *NbenIDA1* homeologs, especially *NbenIDA1A*, showed an expression pattern that perfectly matched the pattern of corolla senescence and abscission of the *N. benthamiana* flower.

5. The pairs of *NbenIDA1* and *NbenIDA2* homeologs with drought response elements in their promoter regions specifically responded to water stress by increasing their expression levels, respectively, in leaf blades and roots.

6. The inoculation of the silencing constructs *clbv3'*-NbenIDA and *clbv3'*-NbenHAE did not produce any obvious effect on plant growth, either affected the rate of development or size of the major vegetative and reproductive organs of the inoculated plants, but arrested corolla abscission.

7. The arrest of corolla abscission in silenced plants was associated with the preservation of the parenchyma tissue at the base of the corolla tube that had virtually collapsed in wild-type corollas.

8. The inoculation of the silencing constructs *clbv3'*-NbenIDA and *clbv3'*-NbenHAE suppressed, respectively, the expression of the *NbenIDA1* pair of homeologs and the receptor *NbenHAE.1* at the base of the corolla tube.

9. The inoculation of the *clbv3'pr*-NbenIDA1 construct increased the expression of *NbenIDA1A* at the base of the corolla tube of *N. benthamiana* flowers, negatively affecting the growth of the inoculated plants and the timing of both corolla senescence and abscission.

10. Taken together, these results suggest that the abscission regulatory module IDA-HAE/HSL2 is conserved in angiosperms.

8
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9
Supplemental data

Supplemental Data S1

Primer name	Sequence (5’ → 3’)
NbenPP2A_F	GACCCTGATGTTGATGTTCGCT
NbenPP2A_R	GAGGGATTTGAAGAGAGATTTC
NbenIDA1A_F	TGAAGCAAGACCAGGAAGAATG
NbenIDA1A_R	GGAACCCCTTTTGGTAGCATAG
NbenIDA1B_F	CCAAAAGGGGTTCCAATTCCTC
NbenIDA1B_R	GAGGTGAAGAGTCCACAAAAGC
NbenIDA2A_F	ATCAATGGTGGCAACGACGA
NbenIDA2A_R	TTGAGCCAATCACCTTTCAAATATTCAT
NbenIDA2B_F	GATCAATGGTGACAACAACAG
NbenIDA2B_R	TGAACCAATTTTCTTTCAGATTCTTTT
NbenIDA3A_F	TCTTGGCTGATTATCACCATGC
NbenIDA3A_R	AAGGAGCAGAAGGTGGAATAGG
NbenIDA3B_F	TGTTAAGCCATTGCCTAATTCCC
NbenIDA3B_R	CCATTGTGCCTTTTCGAAGGAG
NbenIDA4_F	GGCAACGCACACACAATTTC
NbenIDA4_R	TGATACCATTGTGCCGTTGG
NbenIDA5A_F	CCCAAGTAGCCAAAGAAACTCTC
NbenIDA5A_R	TTTCTTGATGGACCAGAAGCTG
NbenIDA5B_F	GTCATTGTCATGGTTCAAGAAGC
NbenIDA5B_R	GGCAACAAGTTCCAAAAATGGC
NbenHAE.1_F	AATTGGGACTTTGCCAGTGC
NbenHAE.1_R	TGCAAGCTGAGTGGAATTGC
NbenHAE.2_F	TTGCTGAACAGTTGCAAGGC
NbenHAE.2_R	ACATCGCGGTGTACAATTGG
NbenHSL2.1_F	TATAGCTTTGGCGTGGTCCTG
NbenHSL2.1_R	CGACTAGCCGGTTCAAATCAAG
NbenHSL2.2_F	ACTGCATTTCAACGGGTTGG
NbenHSL2.2_R	TGCCCGCTTTTCAGTTTGAC

Supplemental Data S2

The DNA and protein sequences of the Solanaceae *IDA*-like and *HAE*-like gene families, as well as the localization of the sequences in the genomes in SolGenomics and the sequence IDs are shown below.

Tomato (*Solanum lycopersicum*) *IDA*-like and *HAE*-like gene families

Gene name	SlycIDA1
SolGenomics source	Tomato genome chromosomes (Build SL3.0)
SolGenomics sequence ID	Solyc05g010000.1.1
SolGenomics chromosome	SL3.0ch05
CDS	ATGGCTTTCTCTTTTTCTTCTTCAAAAACCCTTTATTTATCAAGCAAATTAACTTGTTTGATACTTGTTATTTCTCTACTTTTTAAT TATGGTCATATTGTTGAAGCATCAAGATTTGGGAGAATTATGATGGTAGAGGAAAATTCAAGAATATTTTCATCACAACATATGAAG GTATACAAAAAAGAAAATGCATACAAAGTTGATAATTTATTATTTACTATGTTACCAAAAGGGATTCCAATTCCTCCTTCTGCTCCA TCAAAGAGACATAATGCTATTGAAGACTCTACACCTCAAAATTGA
peptide	MAFSFSSSKTLYLSSKLTCLILVISLLFNYGHIVEASRFGRIMMVEENSRIFSSQHMKVYKKENAYKVDNLLFTMLPKGIPIPPSAP SKRHNAIEDSTPQN*
Gene start	4200134
Gene end	4200439
Strand	1
Gene name	SlycIDA2
SolGenomics source	Tomato genome chromosomes (Build SL3.0)
SolGenomics sequence ID	–
SolGenomics chromosome	SL3.0ch06
CDS	ATGTTGAAAAAAAATCACAACACAACACTATTAATTTATTTACTTCTTGTGATTTTGGTGGTTGATCATCATGATCACCATGTTAAT GCAGTAAAAAACTCACAAGTTGTTAATGTTAAGCCCTTATTACCTAGTAATAACAATTCTAAATCATCTTTTTCTCAATCTTTGCCA AAAGGAGTCCCTATTCCACCTTCTGCTCCTTCCAAAAGGCACAATCAAATCAATATATGA
peptide	MLKKNHNTTLLIYLLLVILVVDHHDHHVNAVKNSQVVNVKPLLPSNNNSKSSFSQSLPKGVPIPPSAPSKRHNQINI*
Gene start	38623220
Gene end	38623453
Strand	1
Gene name	SlycIDA3
SolGenomics source	Tomato genome chromosomes (Build SL3.0)
SolGenomics sequence ID	–
SolGenomics chromosome	SL3.0ch04
CDS	ATGGAAAAAATGAGCATAAAAAACACAACTACAATATCAATCATTTTTGTCCTTGTGATAATAATTCAACATGCTCATGGTGCAAGT CACACACAATTTTTCAAGGTGAAGCCTTTGCCAATTAGTAATAAAAACAATAAATCTCCTTATTATGAGTCTTTGCCAAAAGGAGTC CCAATTCCACCTTCTTCTCCTTCAAAAAGACACAATGGAATCAACCTCAAAAGGTATTGGCCATGA
peptide	MEKMSIKNTTTISIIFVLVIIIQHAHGASHTQFFKVKPLPISNKNNKSPYYESLPKGVPIPPSSPSKRHNGINLKRYWP*
Gene start	5799910
Gene end	5800149
Strand	1
Gene name	SlycIDA4

SolGenomics source	Tomato genome chromosomes (Build SL3.0)
SolGenomics sequence ID	Solyc07g044890.1.1
SolGenomics chromosome	SL3.0ch07
CDS	ATGGCTTATTCTGCTAATTCCAAAACCCTTCATTATATTTCCTCATGGAAATTCATATGCTTGATTCTCACACTATCTCTTGTTCTT GACCATGGACATGGTACTACATGCCCACCTACGCCGTCACGTATGCCGAGGCGTTTGAAAGAGGAAGCTTCTAGAATGTTCTCAGAA CTTTCTGATGAAAAGAAAGAGTTCCTCAGCAGTACTAGTAACCGGTTCCATATGCTACCAAAAGGGATTCCTATTCCTCCTTCTGCA CCATCAAAAAGGTGCAATTAA
peptide	MAYSANSKTLHYISSWKFICLILTLSLVLDHGHGTTCPPTPSRMPRRLKEEASRMFSELSDEKKEFLSSTSNRFHMLPKGIPIPPSA PSKRCN*
Gene start	58068277
Gene end	58068558
Strand	-1
Gene name	SlycIDA5
SolGenomics source	Tomato genome chromosomes (Build SL3.0)
SolGenomics sequence ID	Solyc05g007040.1.1
SolGenomics chromosome	SL3.0ch05
CDS	ATGGCTTATTCTACTACTAATTATTCTTCATGGAAATTCATGTACTTAATTCTCACATTATCTCTTGTTCTTGGCTATGCTTCTTCA GTGAGAATATCGTCGACGATGAATTCAAAAGATGAAGACGCTTATACACTATTTTCAGAACCATCTCCAAAATATGAAGACGCTTAT ACACTATTTTCAGAATCATCTCCGAGATATTACGATGAAAATGAAAAGAAAGAGTTTCAAAAGAGTAATTTGTTTCATATGCTACCA AAAGGGACTCTAATTCCTCCTTCTGGACCATCACGTAGACACAATGGAGATGGTGACTTATCTAATTATCCTTAA
peptide	MAYSTTNYSSWKFMYLILTLSLVLGYASSVRISSTMNSKDEDAYTLFSEPSPKYEDAYTLFSESSPRYYDENEKKEFQKSNLFHMLP KGTLIPPSGPSRRHNGDGDLSNYP*
Gene start	1629558
Gene end	1629893
Strand	1
Gene name	SlycIDA6
SolGenomics source	Tomato genome chromosomes (Build SL3.0)
SolGenomics sequence ID	–
SolGenomics chromosome	SL3.0ch09
CDS	ATGAAGAAACAAAGCAGACTTTTTAAGATCCTCCTTTTTCTATTTTTGACCACTCTTTACTATTCTTCGAGTCATGCAATTACGAAT CGAAAGATATTGAATTTGAAGTCTCGAGTTGAAATTAAAACATCTTCAAGTGTTTTTGGTCAAATGTTACCAAAAGGTGTACCAATA CCTCCCTCTGCTCCATCTTGTAGATCAAGTCCTGGCACACCTCCTTCATGTCCCATGGCACAACCAGAGATCGTGGACATTGTTGCG AGCTTCACCCCCTAA
peptide	MKKQSRLFKILLFLFLTTLYYSSSHAITNRKILNLKSRVEIKTSSSVFGQMLPKGVPIPPSAPSCRSSPGTPPSCPMAQPEIVDIVA SFTP*
Gene start	540104
Gene end	540379
Strand	-1
Gene name	SlycIDA7
SolGenomics source	Tomato genome chromosomes (Build SL3.0)
SolGenomics sequence ID	Solyc09g005780.2.1
SolGenomics chromosome	SL3.0ch09
CDS	ATGATGAACGAAAAAAAGAAATTTTTCAAGAGCCTTCTTTTTCTGTTTTTAACAACCCTTTACTATTCTTCAAGTTATGCAATTACG AATCGAAAGATATTGGATTTGAAGTCCGAAATTGAAATTAAAACATCGTCAAGTGTTTTTGGTCAAATGTTACCAAAGGGTGTACCA TTACCTCCATCTGCTCCATCTTGTAGATCAAGTCCTGGCACACCTCCTTCATGTCCCATGGCACAACCAGAGATCGTAGACGTTGTT GAGAGTTTCACCCCCTAA

peptide	MMNEKKKFFKSLLFLFLTTLYYSSSYAITNRKILDLKSEIEIKTSSSVFGQMLPKGVPLPPSAPSCRSSPGTPPSCPMAQPEIVDVV ESFTP*
Gene start	546577
Gene end	546855
Strand	-1
Gene name	SlycIDA8
SolGenomics source	Tomato genome chromosomes (Build SL3.0)
SolGenomics sequence ID	–
SolGenomics chromosome	SL3.0ch11
CDS	ATGATAAGCTTTTTCAGAAGAAAAATACTTGTCTTATGGATGGCTATTATATTAATCTCTATTTTTGGCCATTTTTGTCATGGTTCA AGAAGCAACTCACAAGTATTCAATACAATAAATAACCAAAGAAACTCTTACAATCATGGCCATTTTTGGAACTTATTGCCAAAAAGA ATCCCAATTCCAGCTTCTGGTCCATCAAGAAAACATAATGACATTGGTTTAAAGAGTACTTGGAGATTACCATGA
peptide	MISFFRRKILVLWMAIILISIFGHFCHGSRSNSQVFNTINNQRNSYNHGHFWNLLPKRIPIPASGPSRKHNDIGLKSTWRLP*
Gene start	533813
Gene end	534061
Strand	-1
Gene name	SolycHAE
SolGenomics source	Tomato genome chromosomes (Build SL3.0)
SolGenomics sequence ID	Solyc07g053600.2
SolGenomics chromosome	SL3.0ch07
CDS	ATGCAAATGAAACTTTTACTCTTCTTTCTGAGTACATTCCCTTTGATTTTTGCTTTAAATCAAGATGGGTTGTATCTTCAAAGACTG AAACACTCGTTGTCTAGCTCAGATCAAGGGGTATTTTCTACTTGGTATGAAAATGATCCTACCCCATGTAACTGGACAGGTGTTACC TGTAATGACGCCGGAGATTCTCCCTCCGTTATCGCTGTTAACCTCTCCGGTGCATCTCTTGTCGGACCCTTTCCGGGTTTCCTCTGC CATCTCACTTCACTTTCATCACTCTCACTTTCGAATAATTTTATTAATTCTACTCTTCCGGTTTCTATTTCTGAATGTGGTAGCCTC ACGTACCTTGACATTTCTCAGAATCTCATCGGTGGAACTATCCCTGACACTATTTCCGATCTTCCTTACCTCAGGTACCTTGATCTT AGTGGATGCTATTTTTCAGGGAATATTCCGGCAAGTTTGGGAAGATTCAGGCAACTAGAGACTCTTATTCTGACTGAGAACATTCTA ACTGGTGAAGTTCCAGCTGCATTAGGTAATGTAACGAGTCTCAAGACACTTGAACTTGCTTACAACCCTTTTGCACCGAGTCTGTTT CCTCCTGAACTCGGTAACTTAACGAATCTTGAGACATTATGGCTAAGCATGTGTAATCTTGTTGGTTCAATCCCAAAAAGTATTGAG AAATTGAGTCGATTGACTAATTTTGATGTGTCCAATAATGGACTAGTTGGGTCAATACCAAGTGCAATTTTCCAGCTTAATAGTATT GTTCAAATTGAGCTCTACAATAATTCTCTTACCGGAAAATTGCCTTCGGGATGGTCTAACTTGACCAGGTTGAGAAGATTCGATGTA TCGACTAACAAGTTAAATGGGACTATTCCTAATGAGTTGTGTGAGCTGCCACTTGAGTCACTCAATCTATTTGAGAATCAATTTGAG GGGCTTATTCCAGAAAGTATAGCTAACTCTCCGAATCTGTATGAGCTGAAGTTATTCTCTAACAGATTTTCTGGTTCATTGCCTAGT GAACTGGGGAAGAACTCGGCTTTACAGTATCTTGATGTTTCATACAATACATTTTCTGGTAAAATTCCTGAAAGTTTATGTGAGATT GGAGCTTTAGAGGATCTTATAGTTATATATAATTCGTTCTCTGGGAATATTCCGGCCAGTCTTGGCAACTGCCGGAGTTTACTTAGG ATCAGGTTCCGGTCTAATAAGCTATTCGGGGAAGTCCCAACTGACTTTTGGAGTTTGCCTCATGTTTATCTCTTGGACCTTTTTGGC AATGCATTTTCAGGAAATATATCACACATGATTTCTGGTGCCAAAAATTTATCTAACCTCCAAATATCAAGAAACAAATTCTCAGGG GTTATACCTAGTGAAGTAGGAAAGTTGAAGAACTTAGTTGAGTTTTCCGCGAGTCATAATGAGCTAACGGGAGAACTTCCAGACACA TTAGTGCAGCTAGGGCAGTTAGGAACCCTTGATCTTAGTTTCAATGAGCTATCAGGGAAAATCCCCTTGGGAATTCACACAATGAAG CAACTCAGTGAGCTTGACTTGGCAAACAATGGATTTTCTGGGGAAATTCCGGAGCAAATTGGGACTTTGCCAGTGCTTAATTATCTT GATCTTTCTGGGAATTACTTCTCAGGGGAAATCCCACTTAGTCTGCAAAGCTTGAAGCTTAATAAGCTAAATTTGTCTAACAATCAG CTGTCAGGGATGATTCCTGCAGTTTTTGATAAGGGTCTTTATAGAGACAGCTTTCGAGGTAATCCAGGTTTGTGTCAAGGTGTTGCT GGTCTTTGTGCTACCAAAGGTAGAGGACAGCATGAAGGATACTTATGGACTTTGAGAGCTATCTACACAGTTGCTGGCTTCGTTTTC CTTGTCGGGATTGCTATGTTCATTTGGAAGTACCAGAAATTCAAGAAGATTAAAAAAGGAAACACTATGACAAAGTGGACATCATTC CATAAGCTTGGATTTAGTGAATTTGAAATACCCGTTGGCCTAGATGAAGCTAATGTAATTGGCAATGGAGCTTCAGGAAGAGTGTAC AAAGCTGTCCTAAGCAATGGTGAGGCAGTAGCTGTCAAGAAGCTATGGGAGAGAACAGTTAAAGATGAAACCCCGTATGGTGCTCTT GAGTCTGATAAAGACGAGTTTGAAATTGAAGTTGAAACTCTGGGTAAAATTAGGCACAAGAATATTGTGAAATTGTGGTGCTGTTGC GATACTGGGGATAGCAAGCTCTTGGTATATGAGTACATGCCAAATGGAAGTTTGGGTGATTTGCTGCACAGTTGCAAGGCCAAATTG TTGGATTGGCCGTTGAGGTTCAAGATAGCTTTAGATGCAGCTGAGGGGCTCTCTTATTTGCACCATGGTTGTGTTCCTCCAATTGTT CACCGTGATGTTAAGTCAAACAACATATTGCTGGATGATGAGTTTGGAGCCAAAATTTCAGATTTTGGTGTGGCAAAAATTGTTAAA GCAGGCAGCAAAGGTGGCGTCGAATCCATGTCTGTAATTGCTGGTTCCTGTGGTTACATTGCTCCAGAGTATGCATATACTCTTCAT GTGAATGAAAAAAGTGACATATATAGCTTTGGAGTGGTCATTTTGGAGCTGGTGACAGGCAAACGACCAGTCAGTCCAGAATTCGGA GAGAAAGATCTAACTACTTGGGTACACACAACGTTGAACGAGAAAGGAGTTGATCAGTTGCTCGATCCAAATCTAAACTCCAGCTTC AAAAAACATATATGCAAGGTTCTTGATGTTGGTCTATGCTGTCTTAACCAGACTCCAGCTAATCGCCCCTCAATGCACAGAGTGGTG AAAATGCTCCAAGAATCAGTTCCTTGTAACGTGCCAGAAATCAAAAACAAGAACGGTAAACTTTCCCCTCAGTACTTTCCAAAGTCA GTCTAG
peptide	MQMKLLLFFLSTFPLIFALNQDGLYLQRLKHSLSSSDQGVFSTWYENDPTPCNWTGVTCNDAGDSPSVIAVNLSGASLVGPFPGFLC HLTSLSSLSLSNNFINSTLPVSISECGSLTYLDISQNLIGGTIPDTISDLPYLRYLDLSGCYFSGNIPASLGRFRQLETLILTENIL

	TGEVPAALGNVTSLKTLELAYNPFAPSLFPPELGNLTNLETLWLSMCNLVGSIPKSIEKLSRLTNFDVSNNGLVGSIPSAIFQLNSI VQIELYNNSLTGKLPSGWSNLTRLRRFDVSTNKLNGTIPNELCELPLESLNLFENQFEGLIPESIANSPNLYELKLFSNRFSGSLPS ELGKNSALQYLDVSYNTFSGKIPESLCEIGALEDLIVIYNSFSGNIPASLGNCRSLLRIRFRSNKLFGEVPTDFWSLPHVYLLDLFG NAFSGNISHMISGAKNLSNLQISRNKFSGVIPSEVGKLKNLVEFSASHNELTGELPDTLVQLGQLGTLDLSFNELSGKIPLGIHTMK QLSELDLANNGFSGEIPEQIGTLPVLNYLDLSGNYFSGEIPLSLQSLKLNKLNLSNNQLSGMIPAVFDKGLYRDSFRGNPGLCQGVA GLCATKGRGQHEGYLWTLRAIYTVAGFVFLVGIAMFIWKYQKFKKIKKGNTMTKWTSFHKLGFSEFEIPVGLDEANVIGNGASGRVY KAVLSNGEAVAVKKLWERTVKDETPYGALESDKDEFEIEVETLGKIRHKNIVKLWCCCDTGDSKLLVYEYMPNGSLGDLLHSCKAKL LDWPLRFKIALDAAEGLSYLHHGCVPPIVHRDVKSNNILLDDEFGAKISDFGVAKIVKAGSKGGVESMSVIAGSCGYIAPEYAYTLH VNEKSDIYSFGVVILELVTGKRPVSPEFGEKDLTTWVHTTLNEKGVDQLLDPNLNSSFKKHICKVLDVGLCCLNQTPANRPSMHRVV KMLQESVPCNVPEIKNKNGKLSPQYFPKSV
Gene start	62148101
Gene end	62151900
Strand	-1
Gene name	SolycHSL1.1
SolGenomics source	Tomato genome chromosomes (Build SL3.0)
SolGenomics sequence ID	Solyc03g006300.1
SolGenomics chromosome	SL3.0ch03
CDS	ATGCATCTTCAAATCTTGCTTATACTTCTATTACCTACATTGATTCTCTCAATAAACCAAGAATCCCTTTATTTACATACCATAAAG CTTGGATTTGATGACCCAAATGGTGTTTTTTCAAACTGGAATCTCCATGATAACTCTTCACCCTGTAACTGGTATGGAGTAAAATGC GACTCTTTAACTCGTTCTGTTACATCTATTGACCTCTCCAATACCAATATCGCCGGCCCATTTCCGGCTTCTCTTCTTTGCCGGCTC AAGTATATTAAGTACATTTCATTCTATAATAACTCTATTAACTCGACACTTCCGGTGGAGGAGTTATCTGCTTGTAAATCTCTTGTC CATCTCGATTTAGCTCAAAATTTGTTAGTGGGTAGTCTTCCATCGAGTTTGGCTGAGCTTCACGAGCTGAAATATCTTGATTTAACC GGGAATAACTTTACCGGCGAAATTCCGGCGAGTTTTGGGGCTTTCCGGCGACTTGAAGTTCTGGGTTTGGTTGAAAATTTGTTAACT GGGACTATCCCGCCGGAGATTGGAAATATTTCGAGTTTGAAACAGCTGAATTTGTCGTACAACCCGTTTTCGCCGGGTCGGGTCCCG CCGGAGATTGGGAACCTTACGAATCTCGAGGTGCTTTGGTTAACTGACTGTGGGTTAATTGGTGAGGTTCCGGGTACATTAAGGGGA TTAAATAAGCTTGTTAACTTGGACCTTGCGTTAAACAACTTGTACGGTCCGATTCCGAGCTGGCTCACTGAGTTAACTAGTGTTGAG CAAATTGAGCTGTATAATAACTCGTTCTCCGGCGAGTTTCCGGTGAATGGGTGGTCGAATATGACATCGTTGAGGCGGGTCGACGTG TCGATGAATCGGGTTACCGGGTCGATCCCGAACGGGTTGTGTGAGTTGCCACTTGAGTCGCTCAATCTTTATGAGAATCAATTGTAT GGTGAGTTACCTGTAGCCATTGCAAATTCACCCAATTTATATGAATTAAAGCTCTTTGGTAATAGTTTGAATGGAACTTTACCTGAA GATCTTGGTAAATTTTCGCCATTGGTATGGATTGATGTTTCAAACAATGAGTTTTCAGGTGAAATTCCGGTGAATTTGTGCGGAAAT GGAGTCTTAGAGGAGGTTTTGATGATAGATAACTCATTTTCCGGTGGAATTCCGCAGAGTTTAAGCCAATGCCGGAGCTTATTACGT GTGAGGTTAGCTCATAATAAGTTCTCAGGTGATGTCCCTGTGGAATTTTGGGGGCTGCCACGCCTCTCGCTGCTTGAGTTAACGAAC AATTCATTTTCTGGTGGAATCGCGAAAACTATAGCTGGTGCATCGAATTTATCAGCTTTGATTTTGTCAAAGAACGAATTTTCGGGT AATATTCCTGAAGAGATTGGCTTTTTGGAAAGTCTGGTTGATTTTGTGGGAAATGATAATAAGTTTTCAGGGTCGTTGCCAGTTAGT ATAGTGAATCTTGAGCAATTGGGAAGAATGGATTTCCACAACAATGAATTAAGTGGTAAGTTTCCTAGTGGGGTTCATTCTTTGAAG AAATTGAATGAATTGAACTTGGCAAACAATGATCTTTCTGGAGAAATTCCCCGAGAAATTGGGAGCTTGTCTGTTTTGAACTATCTT GACCTATCAGGAAACAAGTTTTCGGGGGAAATTCCAGTTGCGTTGCAGAATTTGAAGCTCAATCAGCTGAATTTATCGAATAATGGC CTTTCGGGTGGTATTCCTCCTTCATATGCAAAGGGAATGTACAAGAATAGCTTTCTGGGGAATCCAGGTTTATGTGGAGATATTGGA GGTTTATGTGATGGAAAAGATGAAGGTAAAACTGCTGGTTATGTATGGTTACTGAGATTGCTTTTCGTACCTGCTGTTTTGGTGTTT GTAGTTGGGGTAGTTTCGTTCTATTGGAAGTATAGGAATTACAAGAAAGCAAAAAGGTTGGATAGATCGAAATGGACCTTGACGTCG TTTCATAAGTTAGATTTCAATGAGTTTGAAGTACTGAGAGCTCTAGATGAAGACAACTTGATTGGTAGTGGTTCTTCCGGGAAGGTT TACAAGGTCGTTTTGAGTAATGGTGAGGCTGCTGCTGTGAAAAAACTTTCAAGAAATTCGAAAAAAGTAGATGAGAGTTGTGACATC GAGAAAGGTAAGTATCAGGATGATGGATTTGATGCAGAGGTTGAGACATTGGGCAAAATTCGACACAAGAACATCGTTAGGCTATGG TGTTGTTGTACAACAAGGGGTTGCAAACTTTTGGTTTATGAGTACATGCCTAATGGAAGCTTGGGTGATTTGCTACACAGCAGCAAA AGTGGGTTGTTGGATTGGCCTAAGAGATTTAAGATAGCTACGGATACTGCAGAGGGACTCTCATATTTGCATCATGATTGTGCTCCT CCGATTGTTCACAGAGACTTTAAGTCGAACAATATCTTGTTGGACGGGGAGTTTGGAGCTCGGGTAGCTGATTTTGGTGTGGCAAAG GTGATTGATGTCGATGACAAGGGAACCATGTCTATGTCAGTCATTGCAGGGTCTTGCGGTTATATTGCTCCAGAATATGCATACACA CTTCAGGTGAACGAGAAGAGTGATATATATAGTTTTGGCGTGGTAGTCCTCGAGCTAGTGACAGGGAAACTCCCTGTAGGTCCCGAA TACGGGGAAAAGGATTTGGTGAAGTGGGTTTGCGCTACTCTAGACCAGAAGGGTATAAATCATGTTATTGACCCGAAACTCGACTCT TGTTTCAAGGAGGACATAAGCAAAGTCCTACAAATTGGCCTCCTCTGCACTAGCCCCCTCCCAATCAACCGACCCCCGATGAGAAAA GTCGTAAAAATGCTGCAGGAAGTTGGTGGCGGAGACCAGCTCAAGACAGCGTTAACAGATGGCAAGTTGACCCCTTACTACCACGAA GACGCATCAGATCAAGGAAATGTAGCTTAA
peptide	MHLQILLILLLPTLILSINQESLYLHTIKLGFDDPNGVFSNWNLHDNSSPCNWYGVKCDSLTRSVTSIDLSNTNIAGPFPASLLCRL KYIKYISFYNNSINSTLPVEELSACKSLVHLDLAQNLLVGSLPSSLAELHELKYLDLTGNNFTGEIPASFGAFRRLEVLGLVENLLT GTIPPEIGNISSLKQLNLSYNPFSPGRVPPEIGNLTNLEVLWLTDCGLIGEVPGTLRGLNKLVNLDLALNNLYGPIPSWLTELTSVE QIELYNNSFSGEFPVNGWSNMTSLRRVDVSMNRVTGSIPNGLCELPLESLNLYENQLYGELPVAIANSPNLYELKLFGNSLNGTLPE DLGKFSPLVWIDVSNNEFSGEIPVNLCGNGVLEEVLMIDNSFSGGIPQSLSQCRSLLRVRLAHNKFSGDVPVEFWGLPRLSLLELTN NSFSGGIAKTIAGASNLSALILSKNEFSGNIPEEIGFLESLVDFVGNDNKFSGSLPVSIVNLEQLGRMDFHNNELSGKFPSGVHSLK KLNELNLANNDLSGEIPREIGSLSVLNYLDLSGNKFSGEIPVALQNLKLNQLNLSNNGLSGGIPPSYAKGMYKNSFLGNPGLCGDIG GLCDGKDEGKTAGYVWLLRLLFVPAVLVFVVGVVSFYWKYRNYKKAKRLDRSKWTLTSFHKLDFNEFEVLRALDEDNLIGSGSSGKV YKVVLSNGEAAAVKKLSRNSKKVDESCDIEKGKYQDDGFDAEVETLGKIRHKNIVRLWCCCTTRGCKLLVYEYMPNGSLGDLLHSSK SGLLDWPKRFKIATDTAEGLSYLHHDCAPPIVHRDFKSNNILLDGEFGARVADFGVAKVIDVDDKGTMSMSVIAGSCGYIAPEYAYT LQVNEKSDIYSFGVVVLELVTGKLPVGPEYGEKDLVKWVCATLDQKGINHVIDPKLDSCFKEDISKVLQIGLLCTSPLPINRPPMRK VVKMLQEVGGGDQLKTALTDGKLTPYYHEDASDQGNVA
Gene start	900801

Gene end	904500
Strand	-1
Gene name	SolycHSL1.2
SolGenomics source	Tomato genome chromosomes (Build SL3.0)
SolGenomics sequence ID	Solyc02g077630.2
SolGenomics chromosome	SL3.0ch02
CDS	ATGAAATCTTCAATTTCAATAATGTTTCTTCAAATCTTGGTTACCCTTTTTCTCCCAACTTTGATTTTCTCACTTAATCAAGAAGGT CTTTATTTACATAATGTGAAGCTTGGATTTGATGACCCTGATAATGTTCTTTCAAACTGGAATGAACATGATGATACACCATGTAAC TGGTTTGGTGTTTCATGTGACAAATTTACTCGCTCTGTTACTTCATTGGACCTTTCTAATGCGAATGTTGCTGGTCCTTTTCCCACT CTGCTTTGTCGGTTGAAGAAGCTGCGTTACATTTCCTTGTATAACAACTCGCTTAACAGTACTCTTCTTGAAGATTTTTCTGGGTGT GAAGCAGTAGAGCATCTTGATTTGGCGCAGAATTTCTTGGTGGGTACACTTCCGGCGAGTTTATCTGAGCTCCCAAACTTGAAATAT CTTGACTTGTCGGGTAATAACTTCACCGGAGATATTCCGGTGAGTTTTGGTTCTTTTCAGCAGCTTGAAGTTCTTGGGTTAGTTGGG AACTTGCTTGACGGGAGTATACCGGCGTTTCTCGGGAACGTTACGACGTTGAAGCAGCTGAATCTGTCGTACAACCCGTTTACTACT GGTCGGATCCCGCCGGAGCTGGGAAATCTGACGAATCTTGAGGTTTTGTGGCTTTCTGACTGTAATTTGATTGGGGAAGTTCCTGAC ACATTGGGGAGGTTGAAGAAGATTGTGGATTTGGACCTTGCTGTTAACTACTTGGATGGGCCGATTCCGAGTTGGCTCACTGAGCTG ACTAGTGCTGAACAAATTGAGCTGTATAACAACTCGTTCACCGGCGAGTTTCCGGTGAATGGGTGGTCGAAAATGACGGCGTTGAGG CGAATCGACGTTTCGATGAACCGGTTAACTGGTACGATTCCGAGGGAGTTGTGTGAGCTGCCACTTGAGTCACTCAATCTTTATGAA AACCAGATGTTTGGTGAATTGCCACAAGACATTGCAAATTCACCAAACTTGTATGAGTTGCGCCTTTTTCACAACCGTTTTAATGGG AGTTTACCTCAACATCTTGGAAAAAATTCACCTTTGTTGTGGATTGATGTGTCGGAAAACAATTTTTCTGGTGAAATTCCGGAAAAT TTATGTGGTAAAGGGTTGTTGGAGGAGCTTTTGATGATAAATAACTTACTTTCTGGTGAAATTCCTGCCAGTTTGAGTGAATGCCGG AGCTTACTGCGAGTGAGATTGGCTCATAACCAGTTATCCGGTGATGTTCCGGAGGGGTTCTGGGGTCTGCCTCACCTTTCCCTGCTT GAGCTCATGGACAATTCACTCTCCGGAGATATCGCGAAAACTATAGCTAGTGCTTCAAATTTATCAGCTTTGATTTTGTCTAAGAAC AAATTTTCAGGTTCCATTCCTGAGGAGATTGGTTCTCTGGAAAATCTTCTTGATTTTGTGGGCAATGATAACCAGTTTTCTGGGCCT TTACCTGCAAGTCTGGTGATTCTTGGACAATTGGGGAGGCTGGATCTTCACAACAATGAGTTAACTGGTAAGCTTCCGAGTGGGATT CATTCTTTGAAGAAATTGAATGAATTGAACTTGGCAAACAATGATCTTTCTGGAGATATCCCCATGGAGATTGGGAGCTTGTCTGTT TTGAATTATCTTGATCTATCAGGGAACCAGTTTTCAGGGAAAATCCCACTGGAGTTGCAGAATTTGAAGCTCAATCAGCTGAACTTG TCGAATAATGACCTTTCGGGTGATATCCCCCCTGTTTATGCAAAGGAAATGTATAAGAGTAGCTTTTTGGGTAATGCTGGTCTATGT GGAGACATTGAGGGCTTGTGTGAAGGAACAGCTGAAGGTAAAACTGCTGGTTATGTTTGGTTATTGAGGTTACTATTCACCCTTGCT GGAATGGTGTTTGTTATTGGGGTTGCTTGGTTCTACTGGAAGTACAAGAATTTTAAGGAAGCTAAAAGGGCTATTGATAAGTCTAAA TGGACTTTAATGTCGTTTCATAAATTGGGTTTCAACGAGTATGAAATCTTGGATGCTCTTGATGAGGATAACTTAATTGGCAGTGGC TCTTCTGGGAAGGTTTACAAGGTTGTTCTGAGCAAGGGTGACACTGTTGCGGTGAAGAAGATATTGAGAAGTGTGAAAATAGTAGAT GATTGTAGTGATATCGAGAAAGGTAGCATTCAAGAAGATGGATTTGAAGCGGAGGTTGAGACGTTGGGGAAGATTCGACACAAGAAC ATTGTTAAGCTATGGTGTTGTTGTACAACTAGGGATTGCAAACTTCTGGTCTATGAGTATATGCCTAATGGAAGTTTGGGTGATTTG CTACACAGCAGCAAAAGTGGCCTTCTAGACTGGCCTATGAGATATAAGATAGCCATGGATGCAGCTGAGGGACTCTCCTACTTGCAT CATGACTGTGCTCCACCTATCGTTCACAGAGATGTTAAGTCAAATAACATCTTGCTGGATGGTGAGTTCGGAGCTCGTGTTGCTGAC TTCGGTGTTGCAAAGGCGGTCGAAGCTAATGCTAAGGCAATCAAGTCCATGTCTGTTATTGCAGGGTCTTGTGGTTACATTGCTCCA GAATATGCATACACACTGCGGGTGAACGAGAAGAGTGATATATACAGCTTCGGTGTGGTCATCCTAGAGCTTGTAACGGGGAAACGC CCTGTAGATCCCGAGTTTGGGGAAAAGGATCTGGTGAAATGGGTGTGCAGCACGTTGGACCAAAAGGGTGTAGATCATGTCATTGAC CCTAAACTTGATACTTGTTTCAAGGAGGAGATATGCAAGGCCCTAAACATTGGCCTACTCTGCACTAGCCCTCTCCCAATTAACCGA CCCTCGATGAGACGAGTCGTTAAAATGTTGCAAGAAGTAGGTGGTGGAAACCTGCCCAAGGCTGCTTCAAAGGATGGCAAGTTGACA CCTTATTACTATGAAGAAGCATCTGATCAAGGAAGTGTAGCTTAA
peptide	MKSSISIMFLQILVTLFLPTLIFSLNQEGLYLHNVKLGFDDPDNVLSNWNEHDDTPCNWFGVSCDKFTRSVTSLDLSNANVAGPFPT LLCRLKKLRYISLYNNSLNSTLLEDFSGCEAVEHLDLAQNFLVGTLPASLSELPNLKYLDLSGNNFTGDIPVSFGSFQQLEVLGLVG NLLDGSIPAFLGNVTTLKQLNLSYNPFTTGRIPPELGNLTNLEVLWLSDCNLIGEVPDTLGRLKKIVDLDLAVNYLDGPIPSWLTEL TSAEQIELYNNSFTGEFPVNGWSKMTALRRIDVSMNRLTGTIPRELCELPLESLNLYENQMFGELPQDIANSPNLYELRLFHNRFNG SLPQHLGKNSPLLWIDVSENNFSGEIPENLCGKGLLEELLMINNLLSGEIPASLSECRSLLRVRLAHNQLSGDVPEGFWGLPHLSLL ELMDNSLSGDIAKTIASASNLSALILSKNKFSGSIPEEIGSLENLLDFVGNDNQFSGPLPASLVILGQLGRLDLHNNELTGKLPSGI HSLKKLNELNLANNDLSGDIPMEIGSLSVLNYLDLSGNQFSGKIPLELQNLKLNQLNLSNNDLSGDIPPVYAKEMYKSSFLGNAGLC GDIEGLCEGTAEGKTAGYVWLLRLLFTLAGMVFVIGVAWFYWKYKNFKEAKRAIDKSKWTLMSFHKLGFNEYEILDALDEDNLIGSG SSGKVYKVVLSKGDTVAVKKILRSVKIVDDCSDIEKGSIQEDGFEAEVETLGKIRHKNIVKLWCCCTTRDCKLLVYEYMPNGSLGDL LHSSKSGLLDWPMRYKIAMDAAEGLSYLHHDCAPPIVHRDVKSNNILLDGEFGARVADFGVAKAVEANAKAIKSMSVIAGSCGYIAP EYAYTLRVNEKSDIYSFGVVILELVTGKRPVDPEFGEKDLVKWVCSTLDQKGVDHVIDPKLDTCFKEEICKALNIGLLCTSPLPINR PSMRRVVKMLQEVGGGNLPKAASKDGKLTPYYYEEASDQGSVA
Gene start	43076801
Gene end	43080600
Strand	-1
Gene name	SolycHSL2
SolGenomics source	Tomato genome chromosomes (Build SL3.0)
SolGenomics sequence ID	Solyc02g091860.2

SolGenomics chromosome	SL3.0ch02
CDS	ATGGATTACATGAAGCTTCAATTGCTGATACTCATAAGTTTTTTTCTCTTCATTGTTCCGGCGAGTTCATCGCCTCGGGATATTGCT ATTTTACTCCGGGTTAAGTCCGCCCAACTCGATGACCCGAATGGGTTGATTGCTGATTGGAACGGGTCTGCTCCAAATGCGCCTTGC AGCTGGAACGGGATCAAGTGTGATCGTAGAACCGGTCAGGTTCTGTCCATTGATTTTGGGAGTTTTGGAATCGCAGGTCGTTTTCCT GCTGATTTCTGCCGGATTTCGACTTTGCAGGAACTCAATCTGGGTGATAACAGTTTTGGTGAGTCCATTTCCTCTGACTCATGGTCA CTCTGTTCGCATCTACACTTATTGAATATTTCTTTAAATTTCTTTGTTGGCCGGCTGCCGGAGTTTGTTACCAAGTTTGATAACTTG ACCGTCCTTGATGCTAATTCAAACAATTTCTCCGGTGAAATCCCGGCGAGTTTAGGCCGTTTACCCAAATTACAAGTGCTAAATATA GCTAACAATCTCCTCAATGGTTCAATTCCTGAGTTCTTGACGAATCTTACCGAGTTGACTCGATTGGAAATTGCTGCAAATCCGTTT AAGCCAGGTCCATTGCCTTCCTCAATCGGCCGACTCGGTAAGCTTCGAATTTTCTATGCTCGGTTTGCGAGCCTTGTTGGGAATTTT CCAGATTCTATCAAAGACCTGAAATCTATTCAGGATTTTGATGTGGCAAACAACAATCTCTCCGGAAAAATTCCAGAAAGCTTCGGA AAACTCAAAACCATACAACAAATAGAGCTCTTTGGGAACCATTTCTCAGGCGAATTGCCGGACATGTTTTCCGGTCTTGGTTCTCTT TCCAGGTTTGACGCTTCTGAGAACAATCTCACCGGGAAAATACCTGAAACCCTTACCCATTTGCCATTGGAATCTTTAAATCTCAAT GATAACCAATTAGAAGGCGAAATTTCAGAAAATTTAGCTCTTAACCCAAATCTTAGTCAGTTAAAGCTTTTTAACAACAGATTTTCA GGTACTTTACCTCAAACGTTTGGTTTAAGTTCAGATTTAGATGAGTTTGATGTCTCCGGCAACAATCTAGAAGGTTCTTTACCTCCC AACCTATGTTCTAGAAAGAAACTTAGGATTTTGAACCTGTTTGATAATAAGTTCAATGGGCCAATCCCAGAATCCTATGGGCAGTGT TATTCACTATCATATGTGCGTATCTATAACAATCAATTCTCTGGTGAATTACCAACTGGTTTCTGGGGATTTGATGGATACACATTT CTTGAACTGCGAAACAACAACTTTCAAGGTTCAATTCCAGCTTCAATCTCCAATGCTCGAGGCCTGACACAAATTCTCATCTCTGGC AACAACTTCTCCGGAGAATTGCCAGCAGAAATATGCAATTTGGAAGAGGTTGTGTTCATGGACATTAGCAAGAATCAATTATCAGGG CAGTTGCCTTCGTGTATCACAAGATTGAAAAAGTTACAAAAGCTTGATCTTTCACAAAATAGGATCAGGGGTCAAATTCCCAAATCA GTTAGTTCTTGGAATGAATTGACTGAGTTGAGTTTAGCTGACAATCAACTGACCGGTGAAATTCCTGGTGAGCTTGGGATGTTACCG GTCTTAACATACTTAGACCTCGCCTCAAACTTGCTTTCTGGTGAAATTCCATCCGAGCTGAGCAAGCTCAAGCTCAACAAATTCAAT GTATCGAATAACAGGCTGGAAGGGAAAGTGCCACTTGGGTTTGATAACGATTTTTTCGTCTCAGGTTTACTGGGCAATCCGGATCTT TGTAGTCCAGATCTTAAGCCTCTGCCCCAGTGCCGAAGACCTAAAAGTGTAAGCTTGTACTTGGTGTGTATTTTATCAGCTTTTGCC TTCATACTTGTTGGGTCACTTGTTTGTGTCTTACTCAAGGCCAGTAAGCTGCTACCAATCCGTAGCAAACGTAAAAGTGTGTGGAGA ATTACTGCATTCCAACGTGTCGGTTTCACAGAGAGAGACGTGTTAGATGCACTGATAGAAAAAAATCTCATTGGAGCTGGTGGGTCG GGTCGGGTGTACCGGGTCAAATTGAAAAACGGGCAGATGGTTGCGGTGAAGAAACTTTGGGCGGCTAAACGGGAAAGAGAATCCGAG GAGGTGTTCAGGTCAGAGGTGGAGACATTAGGGAGAGTTCGGCATGGAAACATAGTGAAACTATTGTACACTGGCATTGGTGATGAC TTTAGGATATTGGTGTACGAATACATGGAGAATGGAAGCTTAGGAGACGTATTACATGGGGAAAAAGGTGGCTTGTTATTGGATTGG CCGAGGAGATTTGCCATAGCAGTTGGAGCAGCTCATGGATTGGCCTATTTGCACCATGATTCTGTGCCAGCAGTAGTTCACAGAGAT GTTAAGTCTAATAACATTTTGTTGGACGAAGATTTCAGGCCCAAAGTGGCTGATTTTGGGCTAGCCAAGGCAATGCGAGGGGATGCT GAGGAGAGTGATCAAGCCATGTCCCACATTGCTGGTTCCTACGGCTACATTGCACCTGAATATGCCTACACTCTGAAGATCACTGAG AAGAGTGATGTTTATAGCTTTGGTGTGGTACTGTTGGAACTAATAATTGGTAAAAGGCCTAATGACTCCTCTTTCGGAGAGGATAAG GACGTTGTCAAGTGGGTGTTAGAGGTTGCAACATCGTCTAAGAAAGACGAAGGAACTGGCCATATTGTTACGTGCGCAGGTGGTATT CTTGATTTGAATCAGCTAGTTGACCAGAGAATGAATCCATCTGCAAGCGATTACGCAGAGATTAAAAATGTTTTGGATGTGGCTTTG CTTTGCACTTCAGCATTGCCTATCAATAGGCCTTCCATGAGAAGAGTTGTTGAATTGCTGAAGAATATCCCCTCCGCTCGTTCTAAA ACAACGCATTAG
peptide	MDYMKLQLLILISFFLFIVPASSSPRDIAILLRVKSAQLDDPNGLIADWNGSAPNAPCSWNGIKCDRRTGQVLSIDFGSFGIAGRFP ADFCRISTLQELNLGDNSFGESISSDSWSLCSHLHLLNISLNFFVGRLPEFVTKFDNLTVLDANSNNFSGEIPASLGRLPKLQVLNI ANNLLNGSIPEFLTNLTELTRLEIAANPFKPGPLPSSIGRLGKLRIFYARFASLVGNFPDSIKDLKSIQDFDVANNNLSGKIPESFG KLKTIQQIELFGNHFSGELPDMFSGLGSLSRFDASENNLTGKIPETLTHLPLESLNLNDNQLEGEISENLALNPNLSQLKLFNNRFS GTLPQTFGLSSDLDEFDVSGNNLEGSLPPNLCSRKKLRILNLFDNKFNGPIPESYGQCYSLSYVRIYNNQFSGELPTGFWGFDGYTF LELRNNNFQGSIPASISNARGLTQILISGNNFSGELPAEICNLEEVVFMDISKNQLSGQLPSCITRLKKLQKLDLSQNRIRGQIPKS VSSWNELTELSLADNQLTGEIPGELGMLPVLTYLDLASNLLSGEIPSELSKLKLNKFNVSNNRLEGKVPLGFDNDFFVSGLLGNPDL CSPDLKPLPQCRRPKSVSLYLVCILSAFAFILVGSLVCVLLKASKLLPIRSKRKSVWRITAFQRVGFTERDVLDALIEKNLIGAGGS GRVYRVKLKNGQMVAVKKLWAAKRERESEEVFRSEVETLGRVRHGNIVKLLYTGIGDDFRILVYEYMENGSLGDVLHGEKGGLLLDW PRRFAIAVGAAHGLAYLHHDSVPAVVHRDVKSNNILLDEDFRPKVADFGLAKAMRGDAEESDQAMSHIAGSYGYIAPEYAYTLKITE KSDVYSFGVVLLELIIGKRPNDSSFGEDKDVVKWVLEVATSSKKDEGTGHIVTCAGGILDLNQLVDQRMNPSASDYAEIKNVLDVAL LCTSALPINRPSMRRVVELLKNIPSARSKTTH
Gene start	53739501
Gene end	53743100
Strand	1

Potato (*Solanum tuberosum*) *IDA*-like and *HAE*-like gene families

Gene name	StubIDA1
SolGenomics source	Potato PGSC DM v3 superscaffolds
SolGenomics sequence ID	–
SolGenomics superscaffold	PGSC0003DMB000000071
CDS	ATGATGAACAAACAAAGTAAACTTTCGAAGAGCCTTCTTTTTCTGTTTTTGACAACTCTTTACTATTCTTCAAGTCATGCAATTA CTAATCGAAAGCTATTGGATTTGAAGTCTCAAATTGAGATTAAAACATCTTCAAGTGTTTTTGGTCAAATGTTACCAAAAGGTGT ACCAATACCTCCATCTGCTCCATCTTGTAGATCAAGTCCTGGCACACCTCCTTCATGTCTCTCCCCACAACCAGAGATGGTGGAC GATGTTGCGAGCCTCACCCCCTAA
peptide	MMNKQSKLSKSLLFLFLTTLYYSSSHAITNRKLLDLKSQIEIKTSSSVFGQMLPKGVPIPPSAPSCRSSPGTPPSCLSPQPEMVD DVASLTP*

Gene start	251901
Gene end	253000
Strand	-1
Gene name	StubIDA2
SolGenomics source	Potato PGSC DM v3 superscaffolds
SolGenomics sequence ID	–
SolGenomics superscaffold	PGSC0003DMB000000131
CDS	ATGATAAGTTTCTTCACAAGGAAAGTACTTGTTTTATGGATGACTATTATATTAATCTCTATTTTTGGTCATTTTTGTCATGGTT CAAGAAGCAATTCACAAGTATTCAATACAATAAATAGCCAAAGAAACTCTTACAATCATGGCCATTTTTGGAACTTCCTGCCAAA AAGAATCCCAATTCCAGCTTCTGGTCCATCAAGAAAACATAATGACATTGGTTTAAAGAGTACTTGGAGATTACCATGA
peptide	MISFFTRKVLVLWMTIILISIFGHFCHGSRSNSQVFNTINSQRNSYNHGHFWNFLPKRIPIPASGPSRKHNDIGLKSTWRLP*
Gene start	879373
Gene end	879621
Strand	1
Gene name	StubIDA3
SolGenomics source	Potato PGSC DM v3 superscaffolds
SolGenomics sequence ID	PGSC0003DMC400030779
SolGenomics superscaffold	PGSC0003DMB000000243
CDS	ATGGCTTATTCTACTACTAATTATTCTTCATGGAAATTCATGTACTTAATTCTCACACTATCTCTTGTTCTTGGCTATGCTTCTT CAGTGAGAACATCATCGACGATGAATTCAAAAGAGGAAGACGCTTATAGACTATTTTCAGAACCATCTCCGAGATATTACGATGA AAATAAAGTGTTTCAAAAGAGTAATTTGTTTCGTATGCTACCAAAAGGGATTCCAGTTCCTCCTTCTGGACCATCACGTAGGCAC AATGGAGATGTTGACTTTTCTAATTATCCTTAA
peptide	MAYSTTNYSSWKFMYLILTLSLVLGYASSVRTSSTMNSKEEDAYRLFSEPSPRYYDENKVFQKSNLFRMLPKGIPVPPSGPSRRH NGDVDFSNYP*
Gene start	905236
Gene end	905523
Strand	1
Gene name	StubIDA4
SolGenomics source	Potato PGSC DM v3 superscaffolds
SolGenomics sequence ID	–
SolGenomics superscaffold	PGSC0003DMB000000410
CDS	ATGGCTTTCTCTTTTTCTTCTTCAAAAACCCTTTATTTATCAAGCAAATTAATTTGTTTGATACTTGTTATTTCTCTACTTGGTG GTTATGATCATATTGTTGAAGCATCAAGATTTGGGAGAATGATGATTATGGAGGAAAATCAAGAAAAATCAAGAATATTTTCATC ACAACATATGAAGGAATACAAAAAAGAAAATGCATACAAAGTTGATAATTTATTATTTACTATGTTACCAAAAGGGGTTCCAATT CCTCCTTCTGCTCCATCAAAGAGACATAATGCTATTGAGGACTCTACACCTCAAAATTGA
peptide	MAFSFSSSKTLYLSSKLICLILVISLLGGYDHIVEASRFGRMMIMEENQEKSRIFSSQHMKEYKKENAYKVDNLLFTMLPKGVPI PPSAPSKRHNAIEDSTPQN*
Gene start	16621
Gene end	16935
Strand	-1
Gene name	StubIDA5
SolGenomics source	Potato PGSC DM v3 superscaffolds
SolGenomics sequence ID	–

SolGenomics superscaffold	PGSC0003DMB000000420
CDS	ATGGAAAAAATGAGCATAAAAAGCACAACCACAATATCAATCATTTTTGTCCTTGTGATAATTCTACATGCCCATGGTGCAAGTC ACACACAATTTTTCAAGGTGAAGTCTTTGCCAATTAGTAATAAAAACAATAAATCTCCTTATTATGAGTCTTTGCCAAAAGGGGT TCCAATTCCACCTTCTTCTCCTTCTAAAAGACACAATGGAATCAACCTCAAAAGGTTTTGGCCATGA
peptide	MEKMSIKSTTTISIIFVLVIILHAHGASHTQFFKVKSLPISNKNNKSPYYESLPKGVPIPPSSPSKRHNGINLKRFWP*
Gene start	159814
Gene end	160050
Strand	1
Gene name	StubIDA6
SolGenomics source	Potato PGSC DM v3 superscaffolds
SolGenomics sequence ID	–
SolGenomics superscaffold	PGSC0003DMB000000461
CDS	ATGTTGAAAAAAAATCACAACAGAACACTATTAATTTATTTGCTTCTTGTGATTTTGGTGGTTGATCATAATGATCACCATGCTA ATGCAGTAAAAAACTCACAAGTTGTTAATGTTAAGCCCTTATTACCTAATAATAACAATTCCAAATCATCATTTTCTCAATCTTT GCCAAAAGGGGTCCCTATTCCACCTTCTGCTCCTTCCAAAAGGCACAATCAAATCAATATATGA
peptide	MLKKNHNRTLLIYLLLVILVVDHNDHHANAVKNSQVVNVKPLLPNNNNSKSSFSQSLPKGVPIPPSAPSKRHNQINI*
Gene start	377302
Gene end	377535
Strand	1
Gene name	StubIDA7
SolGenomics source	Potato PGSC DM v3 superscaffolds
SolGenomics sequence ID	–
SolGenomics superscaffold	PGSC0003DMB000000592
CDS	ATGGCTTATTCTCTTAATTCCAAAACCCTTCATTATTTTTCCTCATGGAAATTCATATGCTTGATTCTCACACTATCTCTTGTTC TTGACCATGGTAGTGCATGCCCACCGACGGCGTCACGGATGCCGAGGCGTTTGAAAGAGGAAGCTTCTAGAATGTTTTCCGATGA AAAGAAAGAGTTTCTCAAGAGTATTAAATTGTTCGATATGCTACCAAAAGGGGTTCCTATTCCTCCTTCTGCACCATCAGAAAGG TGCAATTAA
peptide	MAYSLNSKTLHYFSSWKFICLILTLSLVLDHGSACPPTASRMPRRLKEEASRMFSDEKKEFLKSIKLFDMLPKGVPIPPSAPSER CN*
Gene start	149451
Gene end	149714
Strand	1
Gene name	StubHAE
SolGenomics source	Potato PGSC DM v3 superscaffolds
SolGenomics sequence ID	PGSC0003DMP400016577
SolGenomics superscaffold	PGSC0003DMS000001958
CDS	ATGCAAATGAAACTATTACTCTTCTTTCTGAGTACATTCCCTTTGATTTTTGCTTTAAATCAAGATGGGTTGTATCTACAAAAAC TGAAACACTCTTTGTCAAGCTCAGATCAAGGGGTATTTTCTACTTGGTATGAAAATGATCCTACCCCATGTAACTGGACAGGTGT CACCTGTAATGACGCCGGAGATTCTCCTTCCGTCGTCGCTGTTAACCTCTCCGGTGCTTCTCTCGCCGGAACCTTTCCGGTCTTC CTCTGCCATCTTACTTCGCTTTCGTCACTCTCGCTTTCGAATAATCTTATTAATTCTACTCTTCCGGTTTCTATTTCTGAATGCC GTAGCCTCACGTACCTTGACCTTTCTCAGAATCTCATCGGTGGAACTATCCCCGACACTATTTCCGATCTTCCTTACCTCAGGTA CCTTGATCTTAGTGGATGCTATTTTTCGGGGAATATTCCGGCAAGTTTCGGAAGATTCAGGCAACTGGAGACTCTTATTCTGACT GAGAACATTCTTACTGGTGAAGTTCCTCCTGCATTAGGTAATGTAACGAGTCTCAAGACACTTGAACTTGCTTACAACCCTTTTG CGCCGAGTCAGTTTCCTCCTGAACTCGGTAACTTGACGAATCTTGAGACATTATGGCTAAGTATGTGTAATCTTGTTGGTTCAAT TCCAAAAAGTATTGAGAAATTGAGTCGATTGACTAATTTTGATGTGTCCAATAATGGACTGGTTGGGTCAATACCAAGTGCAATT TTCCAACTTAATAGTATTGTTCAAATTGAGCTCTACAATAATTCCCTCACCGGAGAATTGCCTTCGGGATGGTCTAACTTGACCA GGTTGAGAAGATTCGATGTGTCGACTAACAAGTTAAATGGGACTATTCCTGATGAGTTGTGTGAGTTGCCACTTGAGTCACTCAA TTTATTTGAGAATCAATTTGAGGGGTTTCTTCCAGAAAGTATAGCTAACTCTCCGAATCTGTATGAGCTTAAGTTATTCTCTAAC

	AGATTTTCTGGTTCATTGCCTAGTGAACTGGGGAAGAACTCGGCTTTACAGTATCTTGATGTTTCATACAATACATTTTCTGGTA AAATTCCTGAAAGTTTGTGTGAGATGGGAGCTTTAGAGGATCTTATAGTGATATATAATTCGTTCTCTGGGAGTATTCCGGCTAG TCTTGGCAACTGCCGGAGTTTACTTAGGGTCAGGTTTCGGGATAATAAGCTATTCGGGGAAGTCCCAACTGAGTTTTGGAGTTTG CCTCAGGTTTATCTCTTAGACCTTTTTGGCAATGCATTTTCAGGAAATATATCACACATGATTTCTGGTGCCAAAAATTTGTCTA ACCTACAAATATCAAGAAACAAATTCTCAGGGGTTATACCTAGTGAAGTAGGAAAGTTGAAGAACTTAGTTGAGTTTTCTGCGAG TCATAATGAGCTAACGGGAGAACTTCCAGACACATTAGTGCAGCTAGGGCAGTTAGGTACCCTTGATCTTAGTTTCAATGAGCTA TCAGGGAAAATCCCCTTCGGAATTCACACAATGAAGCAACTCAGTGAGCTTGACTTGGCAAACAATGGATTTTCTGGGGAAATTC CGGAGGAAATTGGGACTTTGCCAGTGCTTAATTATCTTGATCTTTCTGGGAATTACTTCTCAGGGGAAATCCCACTCAGTCTGCA AAGCTTGAAGCTTAATAAGCTAAATTTGTCTAATAATCAGCTGTCAGGGATGATTCCTGCAGTTTTTGATAAGGGTGTTTATAGA GACAGCTTTCGAGGTAATCCAGGTTTGTGTCAAGGTGTTGCTGGTCTTTGTCCTACCAAAGGTAGAGGACAGCATGAAGGATACT TATGGACTTTGAGAGCTATCTATACAGTTGCTGGCTTCGTTTTTCTTGTCGGGATTGCTATGTTCATTTGGAAGTATCAGAAATT CAAGAAGATTAAGAAAGGAAACACTATGACAAAGTGGACATCATTCCATAAGCTTGGATTTAGTGAATTTGAAATACCCGTTGGC CTAGATGAAGCTAATGTAATTGGCAATGGAGCTTCAGGAAGAGTGTACAAAGCTGTCCTAAGCAATGGTGAGGCAGTAGCTGTCA AGAAGCTATGGGAGAGAACAGTTAAAGATGAAACCCCTTATGGTGCTCTTGAGTCTGATAAAGACGAGTTTGAAATTGAAGTTGA AACTCTGGGTAAAATTAGGCACAAGAATATTGTGAGATTGTGGTGCTGTTGCGTTACTGGGGATAGCAAGCTCTTGGTATATGAG TACATGCCAAATGGAAGTTTGGGCGATTTGCTGCACAGTTGCAAGGCCAAATTGTTGGATTGGCCGTTGAGGTTCAAGATCGCTT TAGATGCTGCTGAGGGGCTTTCTTATTTGCACCATGGTTGTGTTCCTCCAATTGTTCACCGTGATGTTAAGTCAAACAACATATT GCTGGATGATGAGTTTCGGGCCAAAATTTCAGATTTTGGTGTGGCAAAAATTGTTAAAGCAGACAGCAAAGGTGACGTTGAATCC ATGTCTGTAATTGCTGGTTCCTGTGGTTACATTGCACCAGAGTATGCATATACTCTTCATGTGAATGAAAAAAGTGACATATATA GCTTTGGAGTGGTCATTTTGGAGCTGGTGACAGGCAAAAGACCAGTCAGTCCAGAATTCGGGGAGAAAGATCTAGCTACTTGGGT ACACACGACGTTGAACGAGAAAGGAGTTGATCAGTTGCTCGACCCAAATCTAAACTCCAGCTTCAAAGAACATATATGCAAGGTT CTTGATGTTGGTCTACGTTGTCTTAACCAAACTCCAGCTAATCGCCCCTCAATGCACAGAGTGGTGAAAATGCTCCAAGAATCAG CTCCTTATAATGTGCCAGAAATGGAAAACAAGAATGGTAAACTTTCCCCTCACTTTCCAAAGTCAGTCTAG
peptide	MQMKLLLFFLSTFPLIFALNQDGLYLQKLKHSLSSSDQGVFSTWYENDPTPCNWTGVTCNDAGDSPSVVAVNLSGASLAGTFPVF LCHLTSLSSLSLSNNLINSTLPVSISECRSLTYLDLSQNLIGGTIPDTISDLPYLRYLDLSGCYFSGNIPASFGRFRQLETLILT ENILTGEVPPALGNVTSLKTLELAYNPFAPSQFPPELGNLTNLETLWLSMCNLVGSIPKSIEKLSRLTNFDVSNNGLVGSIPSAI FQLNSIVQIELYNNSLTGELPSGWSNLTRLRRFDVSTNKLNGTIPDELCELPLESLNLFENQFEGFLPESIANSPNLYELKLFSN RFSGSLPSELGKNSALQYLDVSYNTFSGKIPESLCEMGALEDLIVIYNSFSGSIPASLGNCRSLLRVRFRDNKLFGEVPTEFWSL PQVYLLDLFGNAFSGNISHMISGAKNLSNLQISRNKFSGVIPSEVGKLKNLVEFSASHNELTGELPDTLVQLGQLGTLDLSFNEL SGKIPFGIHTMKQLSELDLANNGFSGEIPEEIGTLPVLNYLDLSGNYFSGEIPLSLQSLKLNKLNLSNNQLSGMIPAVFDKGVYR DSFRGNPGLCQGVAGLCPTKGRGQHEGYLWTLRAIYTVAGFVFLVGIAMFIWKYQKFKKIKKGNTMTKWTSFHKLGFSEFEIPVG LDEANVIGNGASGRVYKAVLSNGEAVAVKKLWERTVKDETPYGALESDKDEFEIEVETLGKIRHKNIVRLWCCCVTGDSKLLVYE YMPNGSLGDLLHSCKAKLLDWPLRFKIALDAAEGLSYLHHGCVPPIVHRDVKSNNILLDDEFRAKISDFGVAKIVKADSKGDVES MSVIAGSCGYIAPEYAYTLHVNEKSDIYSFGVVILELVTGKRPVSPEFGEKDLATWVHTTLNEKGVDQLLDPNLNSSFKEHICKV LDVGLRCLNQTPANRPSMHRVVKMLQESAPYNVPEMENKNGKLSPHFPKSV
Gene start	121901
Gene end	125200
Strand	-1
Gene name	StubHSL1.1
SolGenomics source	Potato PGSC DM v3 superscaffolds
SolGenomics sequence ID	PGSC0003DMP400022697
SolGenomics superscaffold	PGSC0003DMS000002817
CDS	ATGCATCTTCAAATCTTGCTTATACTTCTATTACCTACATTGATTCTCTCAATAAACCAAGAATCCCTTTATTTACACACCATAA AGCTTGGATTTGATGACCCAAATGGTGTTTTTTCAAACTGGAATCTCCATGATAACTCCTCACCCTGTAACTGGTTTGGAGTAAA ATGCGACTCTTTAACTCGTTCTGTTACATCTATTGACCTCTCCAACACCAATATCGCCGGCCCATTTCCGGCTTCTCTTCTTTGC CGGCTCAAGTATATCAAGTACATTTCATTCTACAATAACTCCATTAACTCGACACTTCCGGTGGAGGAGTTATCCGCTTGTAAAT CTCTTGTCCATCTCGATTTAGCTCAAAATTTGTTAGTGGGTAGTCTTCCATCGAGTTTGGCGGAGCTTCCTGAGCTGAAATACCT TGATTTGACCGGAAATAACTTTACCGGCGAAATTCCGGCGCGTTTTGGGGCTTTCCGGCGACTTGAAGTTCTGGGTCTGGTTGAA AATTTGTTAACTGGGACTATCCCGCTGGAGATTGGAAACATTTCGAGTTTGAAGCAGCTGAATTTGTCGTACAACCCGTTTTCTC CGGGTCGGATCCCGCCGGAGATTGGGAACCTCACGAATCTCGAGGTGCTATGGTTAACTGACTGTGGGTTAATCGGTGAGGTTCC GGGTACATTAAGGGGATTAAATAAGCTTGTTAACTTGGACCTTGCGTTAAACAACTTGTACGGTCCGATTCCGAGCTGGCTCACT GAGTTAACTAGTGTTGAGCAAATTGAGCTGTACAATAACTCGTTTTCCGGCGAGTTTCCGGTGAATGGGTGGTCAGATATGACCT CGTTGAGGCGGGTCGACCTGTCGATGAATCGGGTTACCGGGTCGATCCCGAGCGGGTTGTGTGAGTTGCCACTTGATTCACTCAA TCTTTATGAGAATCAATTGTATGGTGAGTTACCTATAGCCATTGCAAATTCACCCAATTTATATGAATTAAAGCTCTTTGGTAAT AGGCTAAATGGAACTTTACCTAAAGATCTTGGTAAATTTTCGCCATTGGTATGGATTGATGTTTCAAACAATGAGTTTTCAGGTG AAATTCCGATGAATTTGTGCGGAAATGGGGTTTTAGAGGAGGTTTTGATGATAGATAACTCGTTTTCCGGTGGAATTCCGGTGAG TTTAAGCCAATGCCGGAGCTTATTACGTGTGAGATTAGCTCATAATAAGTTCTCAGGTGATGTCCCTGTGGAATTTTGGGGGCTG CCACGCCTTTTGCTGCTTGAGTTAACGGACAATTCATTTTCTGGTGTAATCGCGAAAACTATAGCTGGTGCATCGAATTTATCAG CTTTGATTTTGTCAAAGAACGAATTTTCGGGTAATATTCCTGAAGAGATTGGCTTTTTGGAAAGTTTGGTTGATTTTGTGGGAAA TGATAACAAGTTTTCAGGGTCGTTACCGGTTAGTATAGTGAATCTTGAGCAATTGGGAAGAATGGATTTTCACAACAATGAATTA AGTGGTAAGTTTCCTAGTGGGGTTCATTCTTTGAAGAAATTGAATGAATTGAACTTCGCAAACAATGATCTTTCTGGAGAAATTC CCCGGGAAATCGGGAGCTTGTCTGTTTTGAACTATCTTGACCTATCAGGAAACAAGTTTTCGGGGGAAATTCCAGTTGCGTTGCA GAATTTGAAGCTCAATCAGCTGAATTTATCGAATAATGGCCTTTCGGGTGGTATTCCTCCTTCATATGCAAAGGGAATGTACAAG AATAGCTTTCTGGGGAATCCTGGTTTATGTGGAGATATTGGAGGTTTATGTGATGGAAAAGATGAAGGTAAAACTGCTGGTTATG TATGGTTACTGAGATTGCTTTTCATACTTGCTGTTTTGGTGTTTGTAGTTGGGGTAGTTTCGTTCTATTGGAAGTATAGGAATTA

	CAAGAAAGCAAAAAGGTTGGATAGATCGAAATGGACCTTGACGTCGTTTCATAAGTTAGGTTTCGATGAGTATGAAGTACTGGAA GCTCTAGATGAAGACAACTTGATTGGTAGTGGTTCTTCCGGGAAGGTTTACAAGGTCGTTTTGAGTAATGGTGAGGCTGCTGCTG TGAAAAAACTTTCAAGAAGTTTGAAAAAAACAGATGAGAGTTGTGACATTGAGAAAGGTAACTATCAGGATGATGGATTTGAAGC GGAGGTTGAGACATTGGGCAAGATTCGACACAAGAACATCGTTAGGCTATGGTGTTGTTGTACAACAAGGGGTTGCAAACTTTTG GTTTATGAGTACATGCCTAATGGAAGCTTGGGCGATTTGCTACACAGCAGCAAAAGTGGGTTGTTGGATTGGCCTAAGAGATTTA AGATAGCTATGGATGCTGCAGAGGGACTCTCATATTTACATCATGATTGTGCTCCTCCGATTGTTCACAGAGACTTGAAGTCGAA CAATATCTTGTTGGACGGGGAGTTTGGAGCTCGAGTTGCTGATTTTGGTGTGGCAAAGGCGATTGATGTCGATGACAAGGGAACC ACGTCTATGTCAGTCATTGCAGGGTCTTGCGGTTATATTGCTCCAGAATATGCCTACACACTTCAGGTGAACGAGAAGAGTGATA TATACAGTTTTGGCGTGGTAATCCTCGAGCTAGTGACAGGGAAACTCCCTGTAGGTCCTGAATACGGGGAAAAGGATTTGGTGAA GTGGGTTTGCGCTACTCTAGACCAGAAGGGTATAGATCATGTTATTGACCCGAAACTCGACTCTTGTTTCAAGGAGGACATAAGC AAAGTCCTAAAAATTGGCCTCCTCTGCACTAGCCCCCTCCCAATTAACCGACCCTCGATGAGAAAAGTCGTAAAAATGCTGCAGG AAGTTGGTGGCGGAGACCAGCTCAAGACAGCGTTAACAGATGGCAAGTTGACCCCTTATTACCACGAAGACGCATCAGATCAAGG AAATGTAGCTTAA
peptide	MHLQILLILLLPTLILSINQESLYLHTIKLGFDDPNGVFSNWNLHDNSSPCNWFGVKCDSLTRSVTSIDLSNTNIAGPFPASLLC RLKYIKYISFYNNSINSTLPVEELSACKSLVHLDLAQNLLVGSLPSSLAELPELKYLDLTGNNFTGEIPARFGAFRRLEVLGLVE NLLTGTIPLEIGNISSLKQLNLSYNPFSPGRIPPEIGNLTNLEVLWLTDCGLIGEVPGTLRGLNKLVNLDLALNNLYGPIPSWLT ELTSVEQIELYNNSFSGEFPVNGWSDMTSLRRVDLSMNRVTGSIPSGLCELPLDSLNLYENQLYGELPIAIANSPNLYELKLFGN RLNGTLPKDLGKFSPLVWIDVSNNEFSGEIPMNLCGNGVLEEVLMIDNSFSGGIPVSLSQCRSLLRVRLAHNKFSGDVPVEFWGL PRLLLLELTDNSFSGVIAKTIAGASNLSALILSKNEFSGNIPEEIGFLESLVDFVGNDNKFSGSLPVSIVNLEQLGRMDFHNNEL SGKFPSGVHSLKKLNELNFANNDLSGEIPREIGSLSVLNYLDLSGNKFSGEIPVALQNLKLNQLNLSNNGLSGGIPPSYAKGMYK NSFLGNPGLCGDIGGLCDGKDEGKTAGYVWLLRLLFILAVLVFVVGVVSFYWKYRNYKKAKRLDRSKWTLTSFHKLGFDEYEVLE ALDEDNLIGSGSSGKVYKVVLSNGEAAAVKKLSRSLKKTDESCDIEKGNYQDDGFEAEVETLGKIRHKNIVRLWCCCTTRGCKLL VYEYMPNGSLGDLLHSSKSGLLDWPKRFKIAMDAAEGLSYLHHDCAPPIVHRDLKSNNILLDGEFGARVADFGVAKAIDVDDKGT TSMSVIAGSCGYIAPEYAYTLQVNEKSDIYSFGVVILELVTGKLPVGPEYGEKDLVKWVCATLDQKGIDHVIDPKLDSCFKEDIS KVLKIGLLCTSPLPINRPSMRKVVKMLQEVGGGDQLKTALTDGKLTPYYHEDASDQGNVA
Gene start	272401
Gene end	276100
Strand	1
Gene name	StubHSL1.2
SolGenomics source	Potato PGSC DM v3 superscaffolds
SolGenomics sequence ID	PGSC0003DMP400054963
SolGenomics superscaffold	PGSC0003DMS000000491
CDS	ATGAAATCTTCAATTTCAATAATGTTTCTTCAAATCTTGGTTACCCTTTTGCTCCCAACTTTGATTTTCTCACTTAACCAAGAGG GTCTTTATTTACATAATGTGAAGCTTGGATTTGATGACCCTGATAATGTTCTTTCAAACTGGAATGAATATGATGATACACCATG TAACTGGTTTGGTGTTTCATGTGACCAATTGACTCGCACTGTTACATCATTGGACCTTTCTAATGCTAATGTTGCTGGTCCTTTT CCGACTCTGCTTTGTCGGTTGAAGAAGCTTCGTTACATTTCGTTGTATAACAACTCTGTGAACAGTACTCTTCTTGACGATTTAT CTGGGTGTGAAGCAGTGGAGCATCTTGATTTGGCGCAGAATTTCTTGGTGGGTACACTTCCGGCGAGTTTATCTGAGCTCCCAAA CTTGAAATATCTTGACTTGTCGGGTAATAACTTTACCGGAGATATTCCGGCGAGTTTTGGTTCTTTTCAGCAGCTTGAAGTTCTT GGGTTAGTTGGAAACTTGCTTGACGGGAGTATACCGGCGTTTCTCGGGAACGTTACGACGTTGAAGCAGCTGAATCTGTCGTACA ACCCGTTTACTACGGGTCGGATCCCGCCGGAGCTGGGGAATCTGACGAATCTTGAGGTTTTGTGGCTTTCCGACTGTAATTTGAT TGGGGAAGTTCCTGACACATTGGGGAGCTTGAAGAAGATAGTGGATTTGGACCTAGCTGTTAACTACTTGGATGGGCCGATTCCG AGTTGGCTCACTGAGCTGACTAGTGCTGAACAAATTGAGCTGTATAACAACTCGTTTACCGGGGAGTTTCCGGTGAATGGGTGGT CGAAAATGACGGCGTTGAGGCGAATCGACGTTTCGATGAACCGGGTAACTGGTACGATTCCGAGGGAGTTGTGTGAGCTGCCACT TGAGTCACTCAATCTTTATGAGAACCAGATGTTTGGTGAATTGCCACAAGGCATTGCAACTTCACCAAACTTGTATGAGTTGCGC CTTTTTCACAACCGTTTTAATGGGAGTTTACCTAAACATCTTGGAAAAAATTCACCTTTGTTGTGGATTGATGTGTCAGAAAACA ATTTTTCTGGTGAAATTCCGGAAAATTTGTGTGGGAAAGGGTTGTTGTTGGAGCTTTTGATGATAAATAACTTACTTTCCGGTGA AATTCCGGCGAGTTTGAGTGAATGCCGGAGCTTACTGCGCGTGAGATTGGCACACAACCAGTTATCCGGTGATGTTCCGGAGGGG TTCTGGGGTCTGCCACACCTTTCTCTGCTTGAGCTCATGGACAATTCACTCTCCGGTGATATCGCGAAAACTATAGCCGGTGCTT CAAATTTATCAGCTTTGATTTTGTCTAAGAACAAATTTTCAGGTTCCATCCCAGAGGAGATTGGTTCTCTGGAAAATCTTCTTGA TTTTGTGGGCAATGATAACCAGTTTTCTGGGCCTTTACCTGCAAGCCTGGTGATTCTTGGACAATTGGGAAGGCTGGATCTTCAC AACAATGAGTTAACTGGTAAGCTTCCAAGTGGGATTCATTCTTTGAAGAAATTGAATGAATTGAACTTGGCAAACAATGATCTTT CTGGAGATATCCCCAAGGAGATTGGGAGCTTGTCTGTTTTGAATTATCTTGATCTATCAGGGAACCAGTTTTCAGGGAAAATCCC AGTGGAGTTGCAGAATTTGAAGCTCAATCAGCTGAACTTGTCGAATAATGACCTTTCGGGTGATATTCCCCCTGTTTATGCAAAG GAAATGTATAAGAGTAGCTTTTTGGGGAATGCTGGTTTATGTGGAGACATTGAGGGCTTGTGTGAAGGAACAGCTGAAGGTAAAA CTGCTGGTTATGTTTGGTTATTGAGGTTACTCTTCACCCTTGCTGGATTGGTGTTTGTTATTGGGGTTGCTTGGTTCTACTGGAA GTACAAGAATTTTAAGGAAGCTAAAAGGGCTATTGATAAGTCTAAATGGACTTTGATGTCGTTTCATAAATTGGGTTTCAACGAG TATGAAATCTTGGATGCTCTTGATGAGGACAACTTAATTGGCAGTGGCTCTTCTGGGAAGGTTTACAAGGTGGTTCTGAGCAAGG GTGACACTGTTGCGGTGAAGAAGATTTTGAGAAGTGTGAAAATAGTAGATGAGAGTAGTGATATCGAGAAAGGTAGCTTTCAAGA AGATGGATTTGAAGCAGAGGTTGAGACGTTGGGGAAGATTCGACACAAGAACATTGTTAAGCTATGGTGTTGTTGTACAACTAGG GATTGCAAACTTCTGGTCTATGAGTATATGCCTAATGGAAGTTTGGGTGATTTGCTACACAGCAGCAAAAGTGGCCTTCTAGACT GGCCTATGAGATCTAAGATAGCCATGGATGCAGCTGAGGGACTCTCTTACTTGCATCATGACTGTGCTCCACCTATCGTTCACAG AGATGTTAAGTCAAATAACATCTTGCTGGATGGTGAGTTTGGAGCTCGTGTTGCTGACTTCGGTGTTGCAAAGGCGGTCGATGCC AATGCTAAGGCAATCAAGTCCATGTCTGTTATTGCAGGGTCTTGTGGTTACATTGCTCCAGAATATGCATACACACTGCGGGTGA ATGAGAAGAGTGATATATACAGCTTCGGTGTGGTCATCCTAGAGCTTGTAACGGGGAAACGCCCTGTGGATCCTGAGTTCGGGGA AAAGGATCTGGTGAAATGGGTGTGCAGTACATTGGACCAAAAGGGCATAGATCATGTAATTGACCCTAAACTTGATACTTGTTTC

	AAGGAGGAGATATGCAAGGCCCTAAACATTGGCCTACTCTGCACTAGCCCTCTCCCAATTAACCGACCCTCGATGAGACGAGTCG TTAAAATGTTGCAAGAAGTGGGTGGTGGGAACTTGCCCAAGGCTGCCTCAAAGGATGGCAAGTTGACACCCTATTACTATGAAGA AGCATCAGATCAAGGAAGTGTAGCTTAA
peptide	MKSSISIMFLQILVTLLLPTLIFSLNQEGLYLHNVKLGFDDPDNVLSNWNEYDDTPCNWFGVSCDQLTRTVTSLDLSNANVAGPF PTLLCRLKKLRYISLYNNSVNSTLLDDLSGCEAVEHLDLAQNFLVGTLPASLSELPNLKYLDLSGNNFTGDIPASFGSFQQLEVL GLVGNLLDGSIPAFLGNVTTLKQLNLSYNPFTTGRIPPELGNLTNLEVLWLSDCNLIGEVPDTLGSLKKIVDLDLAVNYLDGPIP SWLTELTSAEQIELYNNSFTGEFPVNGWSKMTALRRIDVSMNRVTGTIPRELCELPLESLNLYENQMFGELPQGIATSPNLYELR LFHNRFNGSLPKHLGKNSPLLWIDVSENNFSGEIPENLCGKGLLLELLMINNLLSGEIPASLSECRSLLRVRLAHNQLSGDVPEG FWGLPHLSLLELMDNSLSGDIAKTIAGASNLSALILSKNKFSGSIPEEIGSLENLLDFVGNDNQFSGPLPASLVILGQLGRLDLH NNELTGKLPSGIHSLKKLNELNLANNDLSGDIPKEIGSLSVLNYLDLSGNQFSGKIPVELQNLKLNQLNLSNNDLSGDIPPVYAK EMYKSSFLGNAGLCGDIEGLCEGTAEGKTAGYVWLLRLLFTLAGLVFVIGVAWFYWKYKNFKEAKRAIDKSKWTLMSFHKLGFNE YEILDALDEDNLIGSGSSGKVYKVVLSKGDTVAVKKILRSVKIVDESSDIEKGSFQEDGFEAEVETLGKIRHKNIVKLWCCCTTR DCKLLVYEYMPNGSLGDLLHSSKSGLLDWPMRSKIAMDAAEGLSYLHHDCAPPIVHRDVKSNNILLDGEFGARVADFGVAKAVDA NAKAIKSMSVIAGSCGYIAPEYAYTLRVNEKSDIYSFGVVILELVTGKRPVDPEFGEKDLVKWVCSTLDQKGIDHVIDPKLDTCF KEEICKALNIGLLCTSPLPINRPSMRRVVKMLQEVGGGNLPKAASKDGKLTPYYYEEASDQGSVA
Gene start	167401
Gene end	171200
Strand	1

Eggplant (*Solanum melongena*) *IDA*-like and *HAE*-like gene families

Gene name	SmelIDA1
SolGenomics source	Eggplant draft genome (release 2.5.1)
SolGenomics sequence ID	–
SolGenomics scaffold	Sme2.5_00993.1
CDS	ATGTTGACAAAAATTCCCAACACTACAACACTATTAGTTTATTTGCTTGTTGTGATGATGTTGGTGGCTGATAATAATTATGCTAAT GCAGAAAAAGACTCACAAATTGTTAATGTTAAACCCTTATTACCTAGTAATAAGAATTCCAAATCATCATTTTCTCAATCTTTGCCA AAAGGAGTCCCTATTCCACCTTCTGCTCCTTCCAAAAGGCACAATCAAATCAATATCTAA
peptide	MLTKIPNTTTLLVYLLVVMMLVADNNYANAEKDSQIVNVKPLLPSNKNSKSSFSQSLPKGVPIPPSAPSKRHNQINI*
Gene start	18248
Gene end	18481
Strand	1
Gene name	SmelIDA2
SolGenomics source	Eggplant draft genome (release 2.5.1)
SolGenomics sequence ID	–
SolGenomics scaffold	Sme2.5_04429.1
CDS	ATGGTAAAAATGATCATAAAAAAGACAACTACAATATCCATCATTTTTATCCTTATGATGATTCAATTACAACATGCTCAAGGTGCA AGTCACACACAATTTTTCAAGATGAAGTCTTTGCCTATTATTAACAAGAATAAGAAGAATAAATCTCCTTATGAGTCTTTGCCAAAA GGGGTACCAATTCCACCTTCTGCTCCTTCTCTAAGACACAATGGAATCAACCCTAAAAGGTTTGGGCCATGA
peptide	MVKMIIKKTTTISIIFILMMIQLQHAQGASHTQFFKMKSLPIINKNKKNKSPYESLPKGVPIPPSAPSLRHNGINPKRFGP*
Gene start	34294
Gene end	34539
Strand	1
Gene name	SmelIDA3
SolGenomics source	Eggplant draft genome (release 2.5.1)
SolGenomics sequence ID	–
SolGenomics scaffold	Sme2.5_04724.1
CDS	ATGATAAGTTTGTTTAGAAGGAAAGTGCTAGTGTTATGGATGGCTATTATATTAATCTCTCTTTTTGGTCATTGTGATGGTTCAAGA AGCAATTCACAAGTATTCAATCCAATAAATAGCCAAAGAAACTCTTACAATCATGGCCATTTTTGGAACTTATTGCCAAAAAGAATC CCAATTCCAGCTTCTGGTCCATCAAGAAAACACAATGACATTGGTTTAAAGAGTACTTGGAGATTACCTTGA

peptide	MISLFRRKVLVLWMAIILISLFGHCDGSRSNSQVFNPINSQRNSYNHGHFWNLLPKRIPIPASGPSRKHNDIGLKSTWRLP*
Gene start	40347
Gene end	40592
Strand	1
Gene name	SmelIDA4
SolGenomics source	Eggplant draft genome (release 2.5.1)
SolGenomics sequence ID	Sme2.5_06686.1_g00003.1
SolGenomics scaffold	Sme2.5_06686.1
CDS	ATGGCTTCTTCTCCTAATTTGAAATTCATGTGTTTGATTCTCACACTCTCTTTTGTTCTTGGCTATGGTACTACATGCCCACCAACG CCGCCGAGGAGTCTGAAAGAGGAAGCTTCTAAGATGTTTCCAGAATCTTCTCATGATAACAAACAATTTCTCAAGAGGACAAATTGC TTCCATATGTTACCAAAAGGGATCCCTATTCCTCCTTCTGCACCATCAGACAGGTGCAACTTATATATCAAATCTTATGTTTAA
peptide	MASSPNLKFMCLILTLSFVLGYGTTCPPTPPRSLKEEASKMFPESSHDNKQFLKRTNCFHMLPKGIPIPPSAPSDRCNLYIKSYV*
Gene start	19811
Gene end	20078
Strand	1
Gene name	SmelIDA5
SolGenomics source	Eggplant draft genome (release 2.5.1)
SolGenomics sequence ID	–
SolGenomics scaffold	Sme2.5_08129.1
CDS	ATGGCCCCCTCTCTTTCTTATTCAAAAAACCTTTATGTTTCAAAAAAATTAATTTGTTTAGTACTTGTAATTTCTCTTCTTGTTGGT TATGGTGTTGAAGGATCAAGATTTGGGAGAATGATGATGGGAAAAAAAGAAGAAAATTCAAGAATATTTTCATCACAAGTACATTTG AAGGTATATAAAAAGGAAAATTCATACAAGATTGATAATTTGATGTTTACTATGCTACCAAAAGGAATTCCGATTCCTCCTAGTGGC CCATCAAAGAGGCATAATGCTATTGAGGACTCCACGCCTCAAAATTGA
peptide	MAPSLSYSKNLYVSKKLICLVLVISLLVGYGVEGSRFGRMMMGKKEENSRIFSSQVHLKVYKKENSYKIDNLMFTMLPKGIPIPPSG PSKRHNAIEDSTPQN*
Gene start	7336
Gene end	7444
Strand	1
Gene name	SmelIDA6
SolGenomics source	Eggplant draft genome (release 2.5.1)
SolGenomics sequence ID	–
SolGenomics scaffold	Sme2.5_09763.1
CDS	ATGGCTTCTTCTCCTAATTTCAAAACCCTGAATTTCATGTGTTTGATTCTCACACTCTCTTTTGTTCTTGGCTATGGTACTACATGC CCACCAACGCCGCCATGGAATCTGAAAGAGGAAGCTTCTAAAACGTTTCCAGAATCTTCTAATGAAAACAAAGAATTTTTCAAGAGG ACTAATTGGTTTCATATGTTACCAAAAGGGATCCCAGTTCCTCCTTCTGCACCATCAGACAGGTGCAACTAA
peptide	MASSPNFKTLNFMCLILTLSFVLGYGTTCPPTPPWNLKEEASKTFPESSNENKEFFKRTNWFHMLPKGIPVPPSAPSDRCN*
Gene start	10983
Gene end	11228
Strand	-1
Gene name	SmelHAE
SolGenomics source	Eggplant draft genome (release 2.5.1)
SolGenomics sequence ID	–

SolGenomics scaffold	Sme2.5_02596.1
CDS	ATGCAAATGAAACTGTTAGTAATCTTCTTTTTCAGTACATTTCCATTGATTTTTGCTTTAAATCAAGATGGGTTGTATCTACAAAGA CTGAAACACTCTTTATCAAGCTCAGACCAAGGGGTGTTTTCTTCTTGGTCTGAAAATGATCCTACCCCTTGTAACTGGACAGGGGTC ACTTGTAACGGCGCCGGAGATTCGCCCTCCGTCGTCGCTGTTAATCTCTCCGGCTCTTCTCTCGCCGGACCTTTTCCGGGTTTCATC TGCCACCTCACTTCGCTTTCATCACTCTCTCTTTCTAATAATATGATTAACTCTACTCTTCCCCTTTCTATTTCTGAATGCCGTAGC CTCACGTACCTAGACCTTTCTCAGAATCTCCTCGGCGGAACTATCCCCGACACGATTTCTGATCTCCCTCACCTCAGGACGGTGCAT AAAGCATCTCGCGATAGTAGGGTCTTGGAAAGGCCGCACCTCGAAGGGTGTGATGTAGAGATGTACCTGGATCTTAGCGGGTGCTAT TTTTCTGGGAATATTCCGGCAAGTTTTGGAAGATTCCGGCAACTGGAGACTCTTATTCTGACCGAGAACATTCTTACTGGTAAAATT CCAGCTGTGTTGGGTAATGTAACGAGTCTCAAGACACTTGAACTCGCTTACAACCCTTTTGCACAGAGTCAGTTTCCTCCTGAACTC GGTAACTTGACGAATCTTGAGACATTATGGCTAAGCATGTGTAATCTTGTTGGTTCAATTCCAAAAAGTATTGAGAAATTGACTCGA TTGACTAATTTTGATGTGTCCAATAATCGACTCGTTGGGTCAATACCAAGTGCACTTTTCCAGCTTAGCAGTATTGTTCAAATTGAG CTCTACAATAATTCCCTTACCGGAGAATTGCCTCCGGGATGGTCTAACTTGACCATGTTGAGAAGATTCGATGTGTCCACTAACAAG TTAAATGGGACTATTCCAGAGGAGTTGTGTGAGTTGCCACTTGAGTCACTCAATTTGTTTGAGAATCAGTTTGAGGGGTTTCTTCCA GAAAGTATAGCTAAGTCTCCGAATCTGTATGAGCTTAAGTTATTCTCTAACAGATTTTCTGGTTCATTGCCTAGTGAACTGGGGAAG AACTCGGCTTTACAGGAGCTTGATGTTTCATACAATAATTTTTCTGGTGAAATTCCTGAAAGTTTGTGTGAGATGGGAGCTTTAGAG GATCTTATAATGATATATAACTCATTCTCTGGGAGTATTCCGGCTAGTCTTGGCAACTGCCGGAGTTTACTTAGGGTCAGGTTTCGG GCTAATAAGCTATTCGGGGAAGTTCCAACTGAGTTTTGGAGTTTGCCTCAGGTTTATCTCTTAGACCTTTTTGGCAATTCATTTTCA GGAAATATATCACCCATGATTTCTGGTGCCAAAAATTTGTCTAACCTACAAATATCAAGAAACAAATTCTCAGGGGTTATACCTAGT GAAGTAGGAAAATTGAAAATTTTGGTTGAGTTCTCCGCGAGTCATAATGAGCTAACGGGAGAAATTCCAGACACATTCGTGCATCTA GGGCAGTTAGGAACCCTTGATCTTAGTTTCAATGAGCTATCAGGGGAACTCCCCTTAGGAATTCACACGATGAAGCAACTCAGTGAG CTTGACTTGGCAAACAATGGATTTTCCGGGGAAATTCCAGAGGAGATTGGGACTTTGCCAGTGCTTAATTATCTTGATCTTTCTAGG AATTACTTCTCAGGGGGGATCCCACTCAGTCTGCAAAGCTTAAAGCTTAATAAGCTAAATTTGTCTAATAATCAGCTGTCCGGGATG ATTCCTGAATTTTTTGATAAGGGTGTTTATAAAGATAGCTTTCTAGGTAATCCAGATTTGTGTCAAGGTATTGCTGGTCGTTGTCCT ACCAAAGGTAGAGGACAGCATGAAGGATACTTGTGGGCTTTGAGAGCTATCTACACAGTTGCTGGTTTCGTTTTTCTTGTTGGGATT GCTACGTTCATTTGGAAGTACCAGAAATTCAAGAAGATTAAGAAAGGAAACACTATGACAAAGTGGACATCATTCCATAAGCTTGGC TTTAGTGAATTTGAAATACCTGATGGTCTAGATGAAGCTAACGTGATCGGAAATGGAGCTTCAGGGAGAGTGTACAAAGCTGTCCTA AGCAATGGTGAGGCAGTAGCTGTCAAGAAGCTATGGGAGAGAACAGTTAAAGATGAAAGCCCTTGTGGTGCTCTTGAGCCTGATAAA GATGAGTTTGAAAGTGAAGTCGAAACTCTTGGTAAAATTAGGCACAAGAATATTGTAAGATTGTGGTGCTGTTGTGATACTGGGGAT AGCAAGCTCTTGGTATACGAGTACATGCCAAATGGAAGTTTGGGCGATTTGCTGCACAGTTGCAAGGCCAAATTGTTGGATTGGCCG TTGAGGTTCAAGATAGCTTTGGATGCTGCTGAGGGGCTCTCTTATTTGCATCATGGTTGTGTTCCTCCAATTGTTCACCGTGATGTT AAGTCAAACAACATATTGCTGGATGACGAGTTTGGAGCCAAAATTTCAAATTTTGGTGTGGCGAAAATTGTTAAAGCAGCCAGCAAA GGTGGCGTTGAATCCATGTCTGTAATTGCTGGTTCCTGTGGTTACATTGCACCAGAGTATGCATATACTCTTCACGTGAATGAAAAA AGTGACATATATAGCTTTGGAGTTGTCATTTTGGAGCTGGTGACAGGCAGAAGACCAGTCGGTCCAGAATTTGGGGAGAAAGATCTA GCTACTTGGGTACGCACAACCTTGAATGAGAAAGGAGTTGATCAGTTGCTCGATCCAAATCTAAATTCCAGCTTCAAAGAACATATA TGCAAGGTTCTTGACGTTGGTCTACGTTGTCTTAACCATATTCCAGCTAATCGCCCCTCAATGCACAGAGTGGTGAAAATGCTCCAA GAATCAGTTCCTTATAATGTGCCAGGGATGGAACACAAGAATGGTAAACTTTCCCCTCAGTTTCCAAAGTCTGTCTAG
peptide	MQMKLLVIFFFSTFPLIFALNQDGLYLQRLKHSLSSSDQGVFSSWSENDPTPCNWTGVTCNGAGDSPSVVAVNLSGSSLAGPFPGFI CHLTSLSSLSLSNNMINSTLPLSISECRSLTYLDLSQNLLGGTIPDTISDLPHLRTVHKASRDSRVLERPHLEGCDVEMYLDLSGCY FSGNIPASFGRFRQLETLILTENILTGKIPAVLGNVTSLKTLELAYNPFAQSQFPPELGNLTNLETLWLSMCNLVGSIPKSIEKLTR LTNFDVSNNRLVGSIPSALFQLSSIVQIELYNNSLTGELPPGWSNLTMLRRFDVSTNKLNGTIPEELCELPLESLNLFENQFEGFLP ESIAKSPNLYELKLFSNRFSGSLPSELGKNSALQELDVSYNNFSGEIPESLCEMGALEDLIMIYNSFSGSIPASLGNCRSLLRVRFR ANKLFGEVPTEFWSLPQVYLLDLFGNSFSGNISPMISGAKNLSNLQISRNKFSGVIPSEVGKLKILVEFSASHNELTGEIPDTFVHL GQLGTLDLSFNELSGELPLGIHTMKQLSELDLANNGFSGEIPEEIGTLPVLNYLDLSRNYFSGGIPLSLQSLKLNKLNLSNNQLSGM IPEFFDKGVYKDSFLGNPDLCQGIAGRCPTKGRGQHEGYLWALRAIYTVAGFVFLVGIATFIWKYQKFKKIKKGNTMTKWTSFHKLG FSEFEIPDGLDEANVIGNGASGRVYKAVLSNGEAVAVKKLWERTVKDESPCGALEPDKDEFESEVETLGKIRHKNIVRLWCCCDTGD SKLLVYEYMPNGSLGDLLHSCKAKLLDWPLRFKIALDAAEGLSYLHHGCVPPIVHRDVKSNNILLDDEFGAKISNFGVAKIVKAASK GGVESMSVIAGSCGYIAPEYAYTLHVNEKSDIYSFGVVILELVTGRRPVGPEFGEKDLATWVRTTLNEKGVDQLLDPNLNSSFKEHI CKVLDVGLRCLNHIPANRPSMHRVVKMLQESVPYNVPGMEHKNGKLSPQFPKSV
Gene start	601
Gene end	4600
Strand	1
Gene name	SmelHSL1
SolGenomics source	Eggplant draft genome (release 2.5.1)
SolGenomics sequence ID	Sme2.5_00787.1_g00015.1
SolGenomics scaffold	Sme2.5_00787.1
CDS	ATGCATCTTCAAATCCTGCTTTTACTTCTATTACCCACATTGATTCTCTCCATAAACCAAGAAACTCTCTATTTGCACACCATACAG CTCGGATTTGATGACCCAAATGGTGTTTTTTCAACCTGGAATCTCCATGATAACTCCTCACCATGTAACTGGTTCGGCATAAAATGC GACTCTTTAACTCGTTCTGTTACATCTATTGACCTCTCTGACAGCAATATCGCCGGCCCATTTCCGGCATCTCTTCTTTGCCGGATG AAGAATATTAAGTACATTTCGTTCTACAATAACTCCATTAACTCAACCCTTCCGGTGGAGGAGTTATCGGGATGTAAATCTCTTGTG CATCTCGATTTAGCTCAGAATCTGTTAGTGGGTAGTCTTCCATCGAGTTTACCAGAGCTTCCTGAGCTGAAATATCTCGACTTGACC GGAAACAACTTTTCCGGTGAAATTCCGGCGAGTTTTGGGGGTTTCCGGCGGCTTGAAGTTCTGGGTCTGGTTGAAAATTTGTTAACC GGGACTATCCCGCCGGAGATTGGAAACATTTCGACTTTGAAACAGCTGAACTTGTCGTACAACCCGTTTTCTCCGGGTCGGATCCCG CCGGAGATTGGGAACCTCACTAACCTCGAGGTGCTTTGGTTAACTGACTGTGGGTTAACCGGTGAGGTTCCGGGTACATTAAGGGGA TTAAATAAGCTTGTTAACTTGGACCTTGCATTAAACAACTTGTACGGTCTGATTCCGAGCTGGCTTACTGAATTAACTAGTGTTCAG

	CAAATCGAGCTGTACAGTAACTCGTTCTCCGGCGAGTTTCCGGCCAATGGGTGGTCGAATATGACGGCGTTGAGGCGGGTCGACGTG TCGATAAACCGGGTCACCGGGTTGATCCCGAATGAGCTGTGTGAGTTGCCACTTGAATCACTCAATCTTTATGAGAATCAATTATAT GGTGAGTTACCTAAAGCCATTGCAAATTCTCCCAATTTATATGAATTAAAGTTGTTTCATAATAGTTTAAATGGAACGTTACCTCAT GATCTTGGTAAATTTTCGCCATTAGTATGGATTGATGTTTCGAATAATGAGTTTTCCGGGGAAATTCCTGTGAATTTGTGTGGAAAT GGGGTATTGGAGGAGGTTTTGATGATAGATAACTCATTTTCCGGTGGGATTCCGGTGAGTTTAAGCCAATGCCGGAGCTTATTACGG GTGAGATTAGCGCGTAATAAGTTCTCAGGCGATGTCCCGGTGGAGTTTTGGGGGCTGCCACGCCTTTCGTTGCTTGAGCTAACGGAC AATTCATTTTCTGGTGGAATCGCGAAAACTATAGCTGGTGCATCAAATTTATCATCTTTGATCTTGTCAAAGAATGAATTTTCGGGT AATATTCCTGAAGAGATTGGTTTTTTGGAGAATCTGGTTGATTTTGTGGGAAATGATAATAAGTTTTTAGGGTCGTTGCCGGTTAAC ATAGTGCATCTTGAGCAGTTGGGAAGACTGGATCTTCATAACAATGAGTTAAGTGGTAAGTTTCCAAGTGGGGTTCATTCTTTGAAG AAATTGAATGAGTTGAACTTGGCAAATAATGACCTTTCTGGAGAAATTCCTCCGGAAATCGGGAGCTTGTCTGTTTTGAACTATCTT GATCTATCAGGAAACAAGTTTTCGGGGAAAATTCCAGTCGAGTTGCAGAATTTGAAGCTCAATCAACTGAATTTATCAAATAATGGC CTTTCGGGTGGTATTCCTCCTTCGTATGCAAAGGGAATGTACAAGAATAGCTTTCTGGGGAATCCCGGTTTATGTGGAGATATTGGA GGTTTATGTGATGGAAAAGATGAAGGTAAAACTGCTGGTTATGTATGGTTACTGATATTGTTTTTTGTACTTGCTGTTCTGGTGTTT GTAGTTGGGGTGGTTTCGTTCTATTGGAAGTATTGGAATTTCAAGAAAGCAAAGAGGATGGATAGATCGAAATGGACTTTGATGTCG TTTCATAAGTTGGGTTTCGATGAGTATGAAATACTAGAAGCTCTAGACGAAGACAACTTGATTGGTAGTGGTTCTTCCGGGAAGGTT TACAAGGTTGTTTTGAGTAATGGCGAGGCTGCTGCTGTGAAAAAACTTTCAAGAAGTTTGCGAATAGCAGATGAGAGTTGTGACATC GAGAAAGGTAACTTCCACGATGATGGATTTGTAGCGGAGGTTGAGACATTGGGCAAGATTCGACACAAGAACATCGTTAGGCTATGG TGTTGTTGTACAACAAAGGGTTGCAAGCTTTTGGTTTACGAGTACATGCCTAACGGAAGCTTGGGTGATTTGTTACACAGCAGCAAA AGTGGGTTGTTAGATTGGCCTTTGAGATGTAAGATAGCTATGGATGCTGCAGAGGGACTCTCCTATTTGCATCATGATTGTTCTCCT CCGATTGTTCACAGAGACTTTAAGTCGAACAACATCTTGTTGGACGCGGAGTTTGGAGCTCGAGTGGCTGATTTTGGTGTGGCAAAG GCGATTGATGTCGGTGACAAGGGAGCCAAGTCTATGTCAGTCATTGCAGGGTCTTGTGGTTATATTGCTCCAGGTCTGTGTCCGATT CTCCAAAAGTCATTCAATATCGGAGGATCTAACATAGGCACAACAACATTTTTGGAGAATCCAAGCAACAGTGTACCTTTTGTGATC ATTCTTTGTTTACATTTGCTTTCTCGTTCTCATACTGCTCCTCCGGTTGAACTAAGTTCTGTTCATGTTGCAGAATATGCCTACACA CTTCGAGTGAACGAGAAGAGTGATATATACAGCTTTGGCGTGGTAATCCTCGAGCTAGTGACAGGGAAACTCCCTGTGGATCCCGAA TACGGGGAAAAGGATCTGGTGAGGTGGGTTTCCGCTACTCTAGACCAGAAGGGTATCGATCATGTCATTGACCCGACGCTCGACTCT TGTTTCAAGGAGGACATATGCAAAGTCCTGAATATTGGCCTCCTCTGCACCAACCCTCTTCCAATTAACCGACCCTCGATGAGAAAG GTTGTAAAAATGCTGCAGGAAGTTGGTGCTGGAAACCAGCTCAAGACAGCGTCAACGGATGGCAAGTTGACCCCTTATTACCACGAA GACGCGTTAGATGAAGGGAATGCAGCTTAA
peptide	MHLQILLLLLLLPTLILSINQETLYLHTIQLGFDDPNGVFSTWNLHDNSSPCNWFGIKCDSLTRSVTSIDLSDSNIAGPFPASLLCRM KNIKYISFYNNSINSTLPVEELSGCKSLVHLDLAQNLLVGSLPSSLPELPELKYLDLTGNNFSGEIPASFGGFRRLEVLGLVENLLT GTIPPEIGNISTLKQLNLSYNPFSPGRIPPEIGNLTNLEVLWLTDCGLTGEVPGTLRGLNKLVNLDLALNNLYGLIPSWLTELTSVQ QIELYSNSFSGEFPANGWSNMTALRRVDVSINRVTGLIPNELCELPLESLNLYENQLYGELPKAIANSPNLYELKLFHNSLNGTLPH DLGKFSPLVWIDVSNNEFSGEIPVNLCGNGVLEEVLMIDNSFSGGIPVSLSQCRSLLRVRLARNKFSGDVPVEFWGLPRLSLLELTD NSFSGGIAKTIAGASNLSSLILSKNEFSGNIPEEIGFLENLVDFVGNDNKFLGSLPVNIVHLEQLGRLDLHNNELSGKFPSGVHSLK KLNELNLANNDLSGEIPPEIGSLSVLNYLDLSGNKFSGKIPVELQNLKLNQLNLSNNGLSGGIPPSYAKGMYKNSFLGNPGLCGDIG GLCDGKDEGKTAGYVWLLILFFVLAVLVFVVGVVSFYWKYWNFKKAKRMDRSKWTLMSFHKLGFDEYEILEALDEDNLIGSGSSGKV YKVVLSNGEAAAVKKLSRSLRIADESCDIEKGNFHDDGFVAEVETLGKIRHKNIVRLWCCCTTKGCKLLVYEYMPNGSLGDLLHSSK SGLLDWPLRCKIAMDAAEGLSYLHHDCSPPIVHRDFKSNNILLDAEFGARVADFGVAKAIDVGDKGAKSMSVIAGSCGYIAPGLCPI LQKSFNIGGSNIGTTTFLENPSNSVPFVIILCLHLLSRSHTAPPVELSSVHVAEYAYTLRVNEKSDIYSFGVVILELVTGKLPVDPE YGEKDLVRWVSATLDQKGIDHVIDPTLDSCFKEDICKVLNIGLLCTNPLPINRPSMRKVVKMLQEVGAGNQLKTASTDGKLTPYYHE DALDEGNAA
Gene start	80801
Gene end	84500
Strand	-1
Gene name	SmelHSL2
SolGenomics source	Eggplant draft genome (release 2.5.1)
SolGenomics sequence ID	Sme2.5_01937.1_g00002.1
SolGenomics scaffold	Sme2.5_01937.1
CDS	ATGGATTACATCAAACTCCATTTATTGATACTCGTTTGTTTTTTTCTCTTCATTGTTCCGGCGAGTTCATCGCCCCGGGATATCGCC ATTTTACTCAGGGTTAAGTCCGGCAACCTCGGTGACCCGAATGGGTTGCTGGCTGATTGGAACGGGTCTGCCCCAAATGCGCCTTGC AGCTGGAACGGCATTCACTGTGATGGGAAAACCGGTCGGGTTGTTTCCATTGATTTCGCAAGTTTTGGAATCTCCGGTCGTTTTCCG GCTGATTTCTGCCGGATTTCGACTTTGGAGAAACTCAATCTGGGTGATAACAGTTTTGGTGAGTCCATTTCCTCTGACTCCTGGTCC CTCTGTTCACATTTACACTTTCTGAATATTTCTTTGAATTTCCTTGTTGGCCCCCTTCCGGAGTTTATTACCAAGTTTGATAACTTG ACCATCCTTGATGTTAATTCAAACAACTTCTCCGGTGAAATTCCGGTGAGCTTAGGCCGGTTACCCAAATTACAACTGCTGAATATA GCCAACAATCTCCTCAATGGTTCAGTTCCTGAGTTCTTGACGAATCTTACCGAGTTGATGCTATTGGAAATAACTGCAAATCCGTTT AAGCCAAGTCCATTGCCTTCTTCAATCGGCCGACTCAGTAAGCTTCGAAATTTCTATGCTGGGTATTCGAATCTTATTGGAAATATT CCAGATTCCATCAAAGACCTGAAGTCTATTCAGAATTTTGATGTGGCAAACAACAATCTCTCTGGAAAAATTCCAGAAAGCTTCGGA GAACTCAAAACCATTCAACAATTAGAGCTCTTTGCAAACCATTTTTCAGGTGAATTGCCGGACATGTTTTCCGGTCTTGATTCTCTT TTCAGGTTTGACGCTTCGGAGAACAAGCTCACTGGGAAAATACCAGAAAGCCTTGCCCATTTGCCGTTGGTGTCTCTAAACCTCAAT GATAACATTTTAGAAGGCGAAATTTCAGAAAATTTAGCTCTTAATCCAAATCTTAGCCAGTTAAAGCTTTTTAACAACAGCTTTTCA GGCGAGTTTGATGTCTCCGGCAACAATCTAGAAGGTTCTTTACCGCCTAACCTATGTTCTAGAAAGAAACTTAGGATTTTGAACCTG TTCGATAATAAGTTCAATGGGCCAATTCCAGAATCCTATGGGGAGTGTTATTCACTAACATATGTGCGTATCTATAACAACCAATTC TCTGGTGAATTACCAAGTGGTTTCTGGGGATTTTCTGGATACACATTTTTTGAACTGCGAAACAATAATTTTCAAGGTTCAATTCCA GCTTCAATCGTCAATGCTCGAGGCCTATCACAAATTCTCATTTCTGGCAACAAATTCTCTGGGGAATTGCCAGCAGAAATATGCAAT TTGGAAGAGGTTGTGATCATGGACATGAGCAAGAATCAATTTTCAGGGGAGCTGCCTTCGTGTATCACAAGGTTGAAAGCATTACAA

	AAGCTTGATATTTCAGAAAATAGGATCAAGGGTCAAATTCCCCAATCAGTTAGTTCTTGGAATGACTTGACTGAATTGAATTTAGCT AACAATCAATTGACAGGTGAAATTCCTGGTGAGCTTGGGATGTTACCGGTCCTAAACTACTTAGACCTGGCTGCAAACTTGCTTTCT GGCAAAATTCCGTCAGAGCTGAGCAGGCTCAAGCTCAACAAATTTAATGGCAATCCGGATCTTTGTAGTCCGGATCTTAAGCCTCTG CCCCAATGTCCAAGACCGAAAAGTGTAAGCTGGTACTTGGTGTGTATTTTATCAGCTCTTGCCTTCATACTTGTTGGATCACTTGTT TGTGTCTTACTCAAGGCCAGAAAGCTGCTACCAATCCGAAGCAAGCGGAAAAGTGTGTGGAGAATTACTGCATTCCAACGCGTTGGT TTCACAGAGAGAGATGTGTTAGCTGCACTGACAGATGACAATCTCATTGGAGCTGGTGGGTCGGGTCAGGTATACAGGGTCAAATTG AAAAATGGGCAGATGGTTGCGGTGAAGAAACTTTGGGCGGCTAAACGGGAAAGAGAATCCGAGGAGGTGTTCAGGTCAGAGGTGGAG ACGTTAGGGAGAGTACGGCATGGAAACATAGTGAAATTATTGTACACTGGCATTGGTGATGACTTTAGGATATTGGTCTACGAATAC ATGGAGAATGGAAGCTTAGGAGATGTATTACATGGGGAAAAAGGTGGCTTGTTGTTGGATTGGCCGAGGAGATTTGCCATAGCAGTT GGAGCAGCTCAAGGATTGGCCTATTTGCACCATGATACTGTGCCTGCAATAGTGCATAGAGATGTTAAGTCTAATAACATTTTGTTG GACGAGGATTTCCAGCCAAAAGTGGCTGATTTTGGGCTAGCTAAGGCAATGCAACGGGATGCTGAGGAGAGTGAGCAAGCCATGTCC CATGTTGCTGGTTCCTACGGCTACATTGCACCTGAGTATGCATACACTCTGAAGATCAATGAGAAGAGTGATGTTTATAGCTTTGGT GTGGTACTGTTGGAACTAATAACTGGTAAAAGGCCTAATGACTCCTCTTTCGGAGAGAACAAGGATATTGTCAAGTGGGTATTGGAG ATTTCAGCATCACCTAAGAAAGAAGGTATTGGCCATATTGTTACATGCTCAAGTGGTACTCTTGATTTGAACCAGATAGTTGACCAG AGAATGAATTCATCTCCAACTGATTACACGGAGATTAAAAATGTTTTCGATGTGGCTTTGCTTTGCACTTCAGCATTGCCCATTAAT AGGCCCTCCATGAGAAGAGTTGTTGAATTGCTGAAGAATATTCCCTCCGCTCGTGCTAAACCAATCCATTAA
peptide	MDYIKLHLLILVCFFLFIVPASSSPRDIAILLRVKSGNLGDPNGLLADWNGSAPNAPCSWNGIHCDGKTGRVVSIDFASFGISGRFP ADFCRISTLEKLNLGDNSFGESISSDSWSLCSHLHFLNISLNFLVGPLPEFITKFDNLTILDVNSNNFSGEIPVSLGRLPKLQLLNI ANNLLNGSVPEFLTNLTELMLLEITANPFKPSPLPSSIGRLSKLRNFYAGYSNLIGNIPDSIKDLKSIQNFDVANNNLSGKIPESFG ELKTIQQLELFANHFSGELPDMFSGLDSLFRFDASENKLTGKIPESLAHLPLVSLNLNDNILEGEISENLALNPNLSQLKLFNNSFS GEFDVSGNNLEGSLPPNLCSRKKLRILNLFDNKFNGPIPESYGECYSLTYVRIYNNQFSGELPSGFWGFSGYTFFELRNNNFQGSIP ASIVNARGLSQILISGNKFSGELPAEICNLEEVVIMDMSKNQFSGELPSCITRLKALQKLDISENRIKGQIPQSVSSWNDLTELNLA NNQLTGEIPGELGMLPVLNYLDLAANLLSGKIPSELSRLKLNKFNGNPDLCSPDLKPLPQCPRPKSVSWYLVCILSALAFILVGSLV CVLLKARKLLPIRSKRKSVWRITAFQRVGFTERDVLAALTDDNLIGAGGSGQVYRVKLKNGQMVAVKKLWAAKRERESEEVFRSEVE TLGRVRHGNIVKLLYTGIGDDFRILVYEYMENGSLGDVLHGEKGGLLLDWPRRFAIAVGAAQGLAYLHHDTVPAIVHRDVKSNNILL DEDFQPKVADFGLAKAMQRDAEESEQAMSHVAGSYGYIAPEYAYTLKINEKSDVYSFGVVLLELITGKRPNDSSFGENKDIVKWVLE ISASPKKEGIGHIVTCSSGTLDLNQIVDQRMNSSPTDYTEIKNVFDVALLCTSALPINRPSMRRVVELLKNIPSARAKPIH
Gene start	7701
Gene end	9900
Strand	1

Pepper (*Capsicum annuum*) *IDA*-like and *HAE*-like gene families

Gene name	CaIDA1
SolGenomics source	Capsicum_annuum_UCD10X_v1.0
SolGenomics sequence ID	–
SolGenomics chromosome	PepperUCD10Xch04
CDS	ATGGAAAAAATGAGCATAAAAACCGCAACCTATATAATATCCATCATTTTGGTTCTTGTGGTAATTCAACATGCATATGGTGCAAGA CACACACAATTTTTCAAGGTGAAGCCTTTGCCTAAGAATTATAATAATAAATCTCCTAATGAGTCTTTGCCAAAAGGGGTACCAATT CCACCTTCTGCTCCTTCTAAAAGGCACAATGGAATCAACCTCAAAAGATTTTGGCCATGA
peptide	MEKMSIKTATYIISIILVLVVIQHAYGARHTQFFKVKPLPKNYNNKSPNESLPKGVPIPPSAPSKRHNGINLKRFWP*
Gene start	178438292
Gene end	178438525
Strand	1
Gene name	CaIDA2
SolGenomics source	Capsicum_annuum_UCD10X_v1.0
SolGenomics sequence ID	–
SolGenomics chromosome	PepperUCD10Xch06
CDS	ATGTTGAAAAAGATTAATAATATAAAATTATTAGTTTATTTGTTTGTTGTGATCTTAGTGGCTGATCATAATCACCATGCTAATGCA GAAAAAAACTCACAAGTTGTTAATGTTAAGCCCTTATTGTCCAGTAACCATAATTCCCACAAATCTTCATTAACATTTTCTCAGTCT TTGCCAAAAGGAGTCCCTATTCCACCTTCTGCTCCTTCCAAAAGGCACAATCAAATCAATATCTAA
peptide	MLKKINNIKLLVYLFVVILVADHNHHANAEKNSQVVNVKPLLSSNHNSHKSSLTFSQSLPKGVPIPPSAPSKRHNQINI*
Gene start	176812434
Gene end	176812673
Strand	-1

Gene name	CaIDA3
SolGenomics source	Capsicum_annuum_UCD10X_v1.0
SolGenomics sequence ID	CA11g02240
SolGenomics chromosome	PepperUCD10Xch11
CDS	ATGGTTTATTCTACCAATTCCAAAACCCTTCATTATCCTTCATGGAAATTCATGTTCTTGATCATCACACTCTCTCTTGTTCTTAGC TATGGTACTGCAACGAGATCAATGGCGATGACAACCACGACGATGACGACGACGATGAATTCGAAAGAGCAGGAAGAAGCTTTTAGG ACATTCTCAGTACCTAATAAGGGTGACACTGGTGAAAAGAAAGAGATTGATGTCAAAGATAAAAATTTGTTCAATACTATGCTACCA AAAGGAATTCCTATTCCTCCTTCTGGACCATCTAAAAGGCACAATTAA
peptide	MVYSTNSKTLHYPSWKFMFLIITLSLVLSYGTATRSMAMTTTTMTTTMNSKEQEEAFRTFSVPNKGDTGEKKEIDVKDKNLFNTMLP KGIPIPPSGPSKRHN*
Gene start	6480406
Gene end	6480714
Strand	1
Gene name	CaIDA4
SolGenomics source	Capsicum_annuum_UCD10X_v1.0
SolGenomics sequence ID	CA11g01800
SolGenomics chromosome	PepperUCD10Xch11
CDS	ATGGCCTCTTCACTCTCTTCTTCAAAATCCCATTATTTTTCAAGTAAAATAATTTGTTTGTTACTTGTCATTTCTCTTCTTCTTGTT GGTTATGGTGTTGAAGCATCAAGATTTGGGAGGAAAATGATGATAGAAGAAAATAATTCAAGATTATTTTCATCTCAACATATGAAG GTATACAAAAAAGAAAATGCATACAAGACTCAAAATTTGCTATTTACTATGTTACCTAAAGGGGTTCCAATTCCTCCTTCTGCTCCA TCAAAGAGACACAATGCCATCGAGGACTGA
peptide	MASSLSSSKSHYFSSKIICLLLVISLLLVGYGVEASRFGRKMMIEENNSRLFSSQHMKVYKKENAYKTQNLLFTMLPKGVPIPPSAP SKRHNAIED*
Gene start	4624209
Gene end	4624499
Strand	1
Gene name	CaIDA5
SolGenomics source	Capsicum_annuum_UCD10X_v1.0
SolGenomics sequence ID	–
SolGenomics chromosome	PepperUCD10Xch11
CDS	ATGTTCTTGATCATCACACTCTCTCTTGTTCTTAGCTATGGTACTGCAACGAGATCAATGGCGATGACAACCACGACGATGACGACG ACGATGAATTCGAAAGAGCAGGAAGAAGCTTTTAGGACATTCTCAGTACCTAATAAGGGTGACACTGGTGAAAAGAAAGAGATTGAT GTCAAAGATAAAAATTTGTTCAATACTATGCTACCAAAAGGAATTCCTATTCCTCCTTCTGGACCATCTAAAAGGCACAATTAA
peptide	MFLIITLSLVLSYGTATRSMAMTTTTMTTTMNSKEQEEAFRTFSVPNKGDTGEKKEIDVKDKNLFNTMLPKGIPIPPSGPSKRHN*
Gene start	6480457
Gene end	6480714
Strand	1
Gene name	CaIDA6
SolGenomics source	Capsicum_annuum_UCD10X_v1.0
SolGenomics sequence ID	CA11g05460
SolGenomics chromosome	PepperUCD10Xch11
CDS	ATGGCTTATTTTTCATGGAAATTCATGTTCTTGATTCTCATACTCTCTCTTGTTCTTGGCTATACTTCTGCAGCGAGATCAATGGCG GCGACAAAGACGACTAAGATGAATTTGAAAGAGAAAAAAACTTCTGGAATATTTTCAGAACCAATTTCGAGAAACTACAATGAAAAG AAAAAGTTTGTCAAGAGTAAATGGTTCCAAATGCTACCAAAAGGAGTTCCTATTCCTCCTTCTGAACCATCACCTAGGCACAATGAT TATATGATCGACTATTATCCTTTCAATGATTATGTGATCGACTATTATCCTTAA
peptide	MAYFSWKFMFLILILSLVLGYTSAARSMAATKTTKMNLKEKKTSGIFSEPISRNYNEKKKFVKSKWFQMLPKGVPIPPSEPSPRHND YMIDYYPFNDYVIDYYP*
Gene start	27920042
Gene end	27920356
Strand	-1

Gene name	CaHAE
SolGenomics source	Capsicum_annuum_UCD10X_v1.0
SolGenomics sequence ID	CA07g84190
SolGenomics chromosome	PepperUCD10Xch07
CDS	ATGCAGATACAGGTGCCACTCTTCGTCTTCTTGATCACTTTCCCGTTGATTACTTTTGGTCTAAACCAAGAAGGATTATACCTACAA CGACTGAAAGATTCTCTCTCCGGCCCCGAAGAAGTATTTTCTACTTGGTCTGAAAATGATCCTACTCCATGTAACTGGACAGGTATC ACCTGCAACGATCCCTCCGTTGTCGCTGTTAATCTCTCCGGTGCTTCTCTTTCTGGACCCTTTCCGAGTTTCATCTGTCATCTCACT TCTCTTGAATCTCTTTCGCTCTCGAATAATCTCATTAACTCTAGTCTTCCGCATTCTATTTCTGAATGCCGGAGTCTTAAGTATCTT GATCTTTCTCAGAACCTTATTGGTGGTACTATTCCTGAGACGATTTCTCATCTTCCTTATCTCAGCTACCTTGATCTTAGCGGGTGC TATTTCACGGGGAACATTCCGGCAAGTTTTGGAAGATTCAGGCAACTGGAGACTCTTATTCTGACTGAGAACATTCTTACTGGTAAA CTTCCAGCAGTTTTAGGTAATGTAACGAGTCTCAAGAGACTTGAACTCGCTTACAACCCGTTTGCACCAAGCCACTTCCTTCCTGAA CTCGGTAACTTGACAAATCTTGAGACATTATGGCTAAGTATGTGTAATCTTGTTGGTTCAATTCCACAAAGTATTGAGAAATTGAGT CATTTGACTAATTTTGATGTGTCCAATAATGGTCTCATTGGGTCAATACCAAGTGCAATTTTACAGCTTAACAGTATTGTTCAAGTT GAGCTATACAATAATTCCCTCACGGGTGTATTGCCCGCGGGATGGTCTAACTTGACTAAATTGAGGAGGCTTGATGTGTCGACTAAC AAGTTAAATGGGACGATTCCTGATGAGTTGTGTGACTTGCCACTCGAGTCACTCAATTTGTTTGAGAATCAATTTGAAGGGTTGTTT CCAGAAAGTATAGCTAAATCTCCGAATCTGTACGAGCTTAAGTTGTTTTCTAACAGATTTTCTGGTTCATTGCCTAGTGAACTTGGA AAGAACTCAGCTTTACAGTATCTTGATGTTTCATACAATAAATTTTCTGGTAGAATTCCTGAAAGTTTGTGTGAAATGGGAGCTCTA GAGGATCTTATAGGGATATATAATTTGTTTTCTGGGAGTATTCCAGACAGTCTTGGCAACTGCCGGAGTTTACTTAGGGTCAGGTTT CGGGCTAATGAGCTATTCGGAGAAGTCCCAACTGAGTTTTGGAGTTTGCCTCGGGTTTATCTTTTAGACCTTTTTGGCAATGCATTT TCAGGAAACATATCACACATGATTTCCGGTGCCAAAAATTTGTCCAACCTACAAATATCAAGAAACAAATTCTCAGGGGTTATACCG AGTGAAATAGGAAAGTTGAAGAGCTTAGTTGAGTTTTCCGCGAGTCATAATGAGCTAAGGGGAGAACTTCCAGACACATTAGTGAAT CTGGGGCAGTTAGGAACCCTTGATCTTAGTTCCAATGAGCTATCAGGGGAAATCCCCTCGGGAATTCACACAATGAAGCAACTTAGT GAGCTTAACTTGGCAAACAATGGATTTTCAGGGGAAATTCCAGAAGAAATCGGGACATTGCCCGTGCTTAATTATCTTGATCTTTCT GGGAATTACTTCTCAGGGGAAATCCCACTCAGTCTGCAAAGCTTGAAGCTTAATAAGCTAAATTTGTCTAATAATCGACTGTCAGGA ACTATTCCTGCAGTTTTTGATAAGGATGTTTATAGAGAGAGCTTTCTAGGTAATCCAGGTTTGTGTCAAGGTGTTACTGGTCTTTGT CCTACCAAAGGTAGAGGACAGCATGAAGGATACTTGTGGACTTTGAGAGCTATCTACACGGTTGCTGGCTTCGTTTTTCTTGTCGGG ATTGGTATGTTCATTTGGAAGTACCAGAAATTCAAGAAGATTAAGAAAGGAATCACTATGACAAAGTGGACATCATTCCATAAGCTT GGATTCAGTGAATTTGAGATACCCGATGGCCTAGATGAAGCTAATGTGATCGGAAATGGAGCTTCAGGAAGAGTGTACAAAGCTGTC CTGAGCAATGGTGAGGCAGTAGCTGTCAAGAAGCTATGGGAGAGAACAGTTAAAGACGAAACCCCTTATGGTGTTGTTGAGTCTGAT AAAGACGAGTTTGAAATTGAAGTTGAAACTCTGGGTAAAATTAGGCACAAGAATATTGTGAGGTTGTGGTGCTGTTGCGATAGCGGG GATAGCAAGCTCTTGGTATATGAGTACATGCCAAATGGAAGTTTGGGCGATTTGCTGCACAGTTGCAAGGCCAAATTGTTGGATTGG CCGTTGAGGTTCAAGATAGCTTTAGATGCAGCTGAGGGGCTTTCGTATTTGCACCATGATTGTGTTCCTCCAATTGTTCACCGTGAT GTTAAGTCAAACAACATATTGCTGGATGATGAATTTGGAGCCAAAATTTCAGATTTTGGTGTTGCGAAAGTTGTTAAAGCAGCCATC AAAGGTGGTGTCGAATCCATGTCTGTTATTGCTGGTTCTTATGGTTACATTGCACCAGAGTATGCATATACTCTTCATGTGAATGAA AAAAGTGATATATATAGCTTTGGAGTGGTCATTTTGGAGCTGGTAACAGGCAGAAGACCAGTTGGTCCAGAATTCGGGGAGAAAGAT CTAGCTACTTGGGTATGCACGACCTTGAACGAGAAAGGAGTTGATCAGTTGCTAGACCCAAATCTAAATTCCAGCTTCAAGGAACAT ATATGCAAGGTTCTTGACGTTGGTCTACGTTGTCTTAACCATGTTCCAGCTAACCGGCCTTCAATGCGCAGAGTGGTGACAATGCTC CAAGAATCAGTTCCTAATAGTGTACCAGGGATGGAAAACAAGAATGGTAAACTTTCCCTTCACTTTCCAAAGTTAGTCTAG
peptide	MQIQVPLFVFLITFPLITFGLNQEGLYLQRLKDSLSGPEEVFSTWSENDPTPCNWTGITCNDPSVVAVNLSGASLSGPFPSFICHLT SLESLSLSNNLINSSLPHSISECRSLKYLDLSQNLIGGTIPETISHLPYLSYLDLSGCYFTGNIPASFGRFRQLETLILTENILTGK LPAVLGNVTSLKRLELAYNPFAPSHFLPELGNLTNLETLWLSMCNLVGSIPQSIEKLSHLTNFDVSNNGLIGSIPSAILQLNSIVQV ELYNNSLTGVLPAGWSNLTKLRRLDVSTNKLNGTIPDELCDLPLESLNLFENQFEGLFPESIAKSPNLYELKLFSNRFSGSLPSELG KNSALQYLDVSYNKFSGRIPESLCEMGALEDLIGIYNLFSGSIPDSLGNCRSLLRVRFRANELFGEVPTEFWSLPRVYLLDLFGNAF SGNISHMISGAKNLSNLQISRNKFSGVIPSEIGKLKSLVEFSASHNELRGELPDTLVNLGQLGTLDLSSNELSGEIPSGIHTMKQLS ELNLANNGFSGEIPEEIGTLPVLNYLDLSGNYFSGEIPLSLQSLKLNKLNLSNNRLSGTIPAVFDKDVYRESFLGNPGLCQGVTGLC PTKGRGQHEGYLWTLRAIYTVAGFVFLVGIGMFIWKYQKFKKIKKGITMTKWTSFHKLGFSEFEIPDGLDEANVIGNGASGRVYKAV LSNGEAVAVKKLWERTVKDETPYGVVESDKDEFEIEVETLGKIRHKNIVRLWCCCDSGDSKLLVYEYMPNGSLGDLLHSCKAKLLDW PLRFKIALDAAEGLSYLHHDCVPPIVHRDVKSNNILLDDEFGAKISDFGVAKVVKAAIKGGVESMSVIAGSYGYIAPEYAYTLHVNE KSDIYSFGVVILELVTGRRPVGPEFGEKDLATWVCTTLNEKGVDQLLDPNLNSSFKEHICKVLDVGLRCLNHVPANRPSMRRVVTML QESVPNSVPGMENKNGKLSLHFPKLV
Gene start	208492114
Gene end	208495762
Strand	1
Gene name	CaHSL1
SolGenomics source	Capsicum_annuum_UCD10X_v1.0
SolGenomics sequence ID	CA02g15510
SolGenomics chromosome	PepperUCD10Xch02
CDS	ATGACATCTTCAATTTCAATAATGTTTCTTCAAATATTGTTTACTCTTTTTCTCCCTGCTTTGGTTTTCTCTCTTAACCAAGAAGGT CTCTATTTACACAATGTGAAACTTGGATTTGATGACCCTGATAATGTTCTGTCTAACTGGAATGAACACGATGATACCCCATGTAAC TGGTTTGGTGTTTCATGTGACCAGTTAACTATGTCTGTTACATCATTGGATTTGTCTAATGCTAATGTTGCTGGTCCTTTTCCTTCT TTGCTTTGTCGGTTGAAGAAGCTTCGCTACATTTCGTTGTACAACAATGAAGTTAATACTACTTTGCCTGAAGATTTTTCTGGGTGT GAAGTATTGGAGCATCTTGATTTGGCTCAGAATTTCTTGGTGGGTACACTTCCGGCGAGTGTAGCTGAGCTGCCTAACTTGAAATAT

	CTTGACTTATCGGGGAATAATTTTACCGGCGATATTCCGGCGAGTTTTGGTACTTTCCGGCAGCTTGAGGTTCTTGGGTTAGTTGGG AACTTGCTTGACGGGACTATACCAGGTTTTTTAGGGAATGTTACGACGTTAAAGCAGCTGAATCTGTCGTACAACCCGTTTTCTACG GGTCGGATCCCGCCGGAGCTGGGTAATCTGATGAATCTCGAGGTGTTGTGGCTTTCCGACTGTAATTTGATTGGTGAAGTTCCTGAT ACGTTGGGAAAGTTGAAGAAGATTGTGGATTTGGACCTTGCTGTAAACTACTTGAATGGGCCGATACCAAGTTGGCTCACTGAGTTG ACTAGTGCTGAACAAATTGAGCTGTATAACAACTCGTTTACCGGCGAGTTACCGGTGAATGGGTGGTCGAAAATGACGGCGTTGAGG CGAATTGACGTTTCGATGAACGGGGTTACTGGTACGATTCCGAAGGAGTTGTGTGAGTTGCCACTTGAGTCGCTCAATCTTTATGAG AATCAAATGTTTGGTGAATTGCCACAAGGCATTGCAAATTCGCGGAATTTGTATGAGTTGCGCCTTTTTCACAACCGTTTTCATGGG AGTTTGCCTAAAGAGCTTGGAAAGAATTCACCGTTGTTGTGGATTGATGTGTCGGAGAATGAATTTTCTGGTGAAATTCCAGAAAAT TTGTGTGGGAATGGGTTCTTGGAGGAGCTTTTGATGATCGGTAACTTACTTTCCGGTGAAATACCGGTGAGTTTGAGTGAATGCAGG AGCTTACTGCGGGTGAGACTGGCTCACAACCAGTTATCTGGTGATGTTCCGGCGGGGTTTTGGGGTTTGCCACACCTTTCCCTGCTT GAGCTCATGGACAATTCACTCACCGGGGATATTGCGAAGACTATAGCTGGTGCGTCAAATTTATCAGCTTTGATTTTGTCCAAGAAC AAATTTTCGGGTTCCATTCCTGAGGAGATTGGTTCATTGGAGAATCTTCTTGATTTTGTTGGTAATAATAACCAGTTTTCTGGGCCT TTGCCTGCAAGTTTGGTGATTCTTGGACAATTGGGAAGGCTGGATCTTCACAACAATGAGTTAACTGGTAAGCTTCCAAGTGGGATT CATTCTTTGAAGAAATTGAATGAATTGAACCTGGCAAACAATGATCTTTCTGGAGAAATCCCCAAGGAAATTGGGAGCTTGTCTGTT TTGAATTATCTTGATCTATCAGGGAACCAGTTTTCAGGGAAAATTCCAGCGGAGTTGCAGAATTTGAAGCTCAATCAGCTGAACTTG TCGAACAATGACCTTTCGGGTGATATCCCCCCTGTTTATGCAAAAGAAATGTATAAGAGTAGCTTTTTGGGGAATGCTGGTCTTTGT GGAGACATTGAGGGCTTGTGTGAAGGAACAGCTGAAGGTAAAACTGCTGGTTATGTTTGGTTATTGAGGTTACTCTTCACCCTTGCT GGATTGGTGTTTGTAGTTGGGGTTGTTTGGTTCTACTGGAAGTATAAGAACTTTAAGGAAGCTAAAAGGGCTATTGATAAGTCTAAA TGGACTTTGATGTCGTTTCATAAATTGGGTTTCAACGAGTATGAAATCTTGGATGCTCTTGATGAGGACAACTTAATCGGCAGCGGC TCTTCTGGGAAGGTTTACAAGGTTGTTCTGAGCAAGGGTGACACTGTTGCAGTGAAGAAGATATTGAGAACTGTGAAAATAGCAGAT GAGAGTAGTGATATCGAGAAAGGTAGCATTCAAGAAGATGGATTTGAAGCTGAGGTTGAGACTTTGGGAAAGATTCGTCACAAGAAC ATTGTTAAGCTATGGTGTTGTTGTACAACTAGGGATTGCAAACTTCTGGTATATGAGTATATGCCTAATGGAAGCTTGGGTGATTTG CTACACAGCAGCAAAAGTGGCCTTCTAGACTGGCCTATGAGATATAAGATAGCCATGGATGCAGCTGAGGGACTCTCTTACTTGCAT CATGACTGTGCTCCACCTATCGTTCACAGAGATGTTAAGTCTAACAACATCTTGCTGGATGGTGATTTTGGAGCTCGAGTTGCTGAT TTCGGTGTAGCAAAGGCGGTCGATGCCAATGCTAATGCCAAGGGAATCAAATCCATGTCTGTTATTGCAGGGTCTTGTGGTTACATT GCTCCAGAATATGCATACACACTGCGGGTGAACGAGAAGAGTGATATATACAGCTTCGGTGTGGTCATCCTAGAGCTTGTGACGGGG AAACGCCCCGTGGATCCTGAGTTCGGGGAAAAGGATCTGGTGAAGTGGGTGTGCAGTACATTGGACCAAAAGGGTGCAGATCATGTA ATTGACCCTAAACTCGATTCTTGTTTCAAGGAGGAGATATGCAAGGCCCTAAATATTGGCCTACTCTGCACTAGCCCTCTCCCAATT AACCGACCCTCGATGAGACGGGTCGTTAAAATGTTGCAAGAAGTTGGTGGTGTCAACCAGCACAAAGCTGCCTCAAAGGATGGCAAG TTGACACCTTATTACTATGAAGAAGCATCAGATCAAGGAAGTGTAGCTTAA
peptide	MTSSISIMFLQILFTLFLPALVFSLNQEGLYLHNVKLGFDDPDNVLSNWNEHDDTPCNWFGVSCDQLTMSVTSLDLSNANVAGPFPS LLCRLKKLRYISLYNNEVNTTLPEDFSGCEVLEHLDLAQNFLVGTLPASVAELPNLKYLDLSGNNFTGDIPASFGTFRQLEVLGLVG NLLDGTIPGFLGNVTTLKQLNLSYNPFSTGRIPPELGNLMNLEVLWLSDCNLIGEVPDTLGKLKKIVDLDLAVNYLNGPIPSWLTEL TSAEQIELYNNSFTGELPVNGWSKMTALRRIDVSMNGVTGTIPKELCELPLESLNLYENQMFGELPQGIANSRNLYELRLFHNRFHG SLPKELGKNSPLLWIDVSENEFSGEIPENLCGNGFLEELLMIGNLLSGEIPVSLSECRSLLRVRLAHNQLSGDVPAGFWGLPHLSLL ELMDNSLTGDIAKTIAGASNLSALILSKNKFSGSIPEEIGSLENLLDFVGNNNQFSGPLPASLVILGQLGRLDLHNNELTGKLPSGI HSLKKLNELNLANNDLSGEIPKEIGSLSVLNYLDLSGNQFSGKIPAELQNLKLNQLNLSNNDLSGDIPPVYAKEMYKSSFLGNAGLC GDIEGLCEGTAEGKTAGYVWLLRLLFTLAGLVFVVGVVWFYWKYKNFKEAKRAIDKSKWTLMSFHKLGFNEYEILDALDEDNLIGSG SSGKVYKVVLSKGDTVAVKKILRTVKIADESSDIEKGSIQEDGFEAEVETLGKIRHKNIVKLWCCCTTRDCKLLVYEYMPNGSLGDL LHSSKSGLLDWPMRYKIAMDAAEGLSYLHHDCAPPIVHRDVKSNNILLDGDFGARVADFGVAKAVDANANAKGIKSMSVIAGSCGYI APEYAYTLRVNEKSDIYSFGVVILELVTGKRPVDPEFGEKDLVKWVCSTLDQKGADHVIDPKLDSCFKEEICKALNIGLLCTSPLPI NRPSMRRVVKMLQEVGGVNQHKAASKDGKLTPYYYEEASDQGSVA
Gene start	127835588
Gene end	127839159
Strand	-1
Gene name	CaHSL2
SolGenomics source	Capsicum_annuum_UCD10X_v1.0
SolGenomics sequence ID	CA02g24590
SolGenomics chromosome	PepperUCD10Xch02
CDS	ATGGATAACATGAAAATCCAATTTCTGTTAGTGATTATTTTTTTTCTGTTCGTTGTTCCGGCGAGTTCATCGGCCAGGGATATCGCC ATTTTACTCCGGGTTAAGTCTGGTCATCTCGGGGACCCAAATGGTTTGCTTGCTAATTGGAATGAGTCTGCTCCAAATGCTCCTTGT AGCTGGACTGGCATTAGCTGTAATCGGAAAACTGGTCAGGTTGTGGCCATTGAGTTTGCAAGTTTTGGAATTTCCGGTCGTTTTCCG GCTGATTTCTGCCGGATTTCGACTTTGCAGAAACTCAATCTGGGTGATAACAGTTTTGGTGATTCTATATCACCTGATTCTTGGTCT CTCTGTTCACATCTTCACTTTCTGAATATTTCTTTGAACTTCTTTGTTGGTCAGTTGCCGGAGTTTATTGCCCAGTTTGATAACTTG ACTGTCCTTGATGTTAATTCGAATAATTTCTCCGGTGAAATTCCAGCGAGTTTGGTCCGTTTACCCAAATTACAACAGCTGAATATA GCTAACAATCTCCTGAATGGTTCAATTCCTGAGTTCTTGACGAATCTTACCGAGTTGACTCGATTGGAAATTGGTTCAAATCCATAT AAGCCAAGCCCACTGCCTTCCTCAATCGGTCGACTCAGTAAACTTCAAGTTCTCTTTTTTCGGTATGCAAATCTTGTTGGAGAAATT CCAGATTCCATTAGAGACCTGAAATCTATTCAGAATTTTGATGCGGCAATTAACAATCTGACGGGAAGAATTCCAGAAAGCTTGGGA GAACTGAAAACCATACAACAAATAGAGCTCTTTGGAAACCATTTTTCAGGTGAATTGCCTGATATATTTTCGGGTCTTGGTTCTCTT TTCATGTTTGACGTTTCTGAGAACAATCTCACAGGAAAAATACCTGAATCCCTTGCCCGTTTGCACCTGATATCTCTGAATCTCAAT GATAACCAGTTAGAAGGCAAAATTCCAGAAAGTTTAGCTCTTAACCCAAATCTTTGTCAGTTCAAGCTCTTTAACAACAGATTTTCA GGTACTTTACCTCAAAATCTTGGTTTTTCAGATTTAGATGAGTTTGATGTCTCCGGCAATAATCTAGAAGGTTCTTTGCCGCCTAAC TTATGTTCTAGAAAAAAGCTTAAGACTTTGAACCTGTTTAATAATAAGTTCAATGGGCCAATCCCAGAATCCTATGGGGAGTGTAAT TCACTAGCATATGTGCGTATCCATGACAACCAATTCTCTGGTGAGTTACCAGCTGGTTTCTGGGGATTAGCTAGATACACATTTCTT GAACTGCGAAACAACAACTTTCAAGGTTCAATTCCAGCTTCAATCTCCAATGCTCGAGGCCTAACACAACTTCTTATCTCTGGCAAT AGATTTTCCGGGGAATTGCCTGCAGAAATATGCAAGTTGGAAGAGGTTGTGATCATGAATATTAGCAAGAATCAATTATCAGGGGAG TTGCCTTCATGTATCACAAGATTGAAAACGTTACAAAACCTCGATCTTTCGGAAAACAGGATCACGGGTCAAATTCCCAAATCAGTT

	AGTTCTTGGAATGACTTGACTGAATTGAATTTAGCTAACAATCAATTGACAGGTGAAATTCCTGGTGAGCTTGGGACGTTACCGGTC TTAACCTACTTAGACCTCGCTGGAAACTTGCTTTCTGGCAAAATTCCATCGGAGCTGAGCAAGCTCAAGCTCAACAAATTCAATGTA TCAAATAACAGGCTTGAAGGGAAAGTGCCTCTTTGGTTGGATGACAATTATTTTGTCTCAGGTTTACGAGGTAACCCGGGTCTTTGT AGTCCGGATCTTAAACCTCTGCCTGAATGCCCAAAACCCAAAAGTGTAAGCTTGTACGTGGTGTGTATTTTATCAGCTTTCGCCTTC ATACTTGTCGGGTCACTTGTTTGCGTTTTACTCAAGGCTAGTAAGCTGCTACCAATCCGGAGCAAGCATAAAAGTGTATGGAGGATT ACTGCATTCCAACGGGTCGGGTTCACAGAGCGAGACGTGTTAGCTGCACTGACAGATGACAATCTCATAGGAGCTGGTGGGTCGGGT CGGGTATACCGGGTCAAACTGAAAAATGGGCAGATGGTAGCGGTGAAGAAACTTTGGGCGGCTAAGAGGGTAAGAGAATCCGAGGAG GTGTTCAGGTCAGAGGTGGAGACATTAGGAAGAGTCCGGCATGGAAACATAGTGAAATTATTGTACACTGGCATTGGTGATGACTTT AGGATATTGGTATACGAATACATGGAGAATGGGAGCTTAGGAGATGTATTACATGGGGAAAAAATTGGATTGCTGTTGGATTGGCCG AGGAGATTTGCCATAGCAGTTGGAGCAGCTCAAGGATTGGCATATTTGCACCATGATTGTGTGCCTGCAATAGTGCACAGAGATGTC AAGTCTAATAACATTTTGTTGGACGAGGATTTCAGGCCCAAAGTGGCTGATTTTGGGTTAGCTAAGGCAATGCAACAGGATACTGAG GGGAGTGATCAGGCCATGTCCCATGTTGCTGGTTCCTACGGCTACATTGCACCTGAATATGCGTACACTCTGAAGATCAATGAGAAG AGTGATGTTTATAGCTTTGGTGTTGTACTGTTGGAACTAATAATTGGTAAAAGGCCTAATGACTCCTCTTTCGGAGAGAACAAGGAC ATTGTCAAGTGGGTGTTAGAGGGTGCACCATCGTCGAAGAAAGGCGAAGGAATTGGCCACATTACAGATGGAAGTAGCATTCTTGAT TTGAACCAGCTAGTTGACCAGAGAATGAATCCATCTTCAAGCAATTACACAGAGATTAAAAATGTTTTTGATGTGGCTTTGCTTTGC ACTTCGGCATTGCCCATTAATAGGCCCTCCATGAGAAGAGTTGTTGAATTGCTGAAGGATAGCTCCTTTCCCCGTCCCAAATAA
peptide	MDNMKIQFLLVIIFFLFVVPASSSARDIAILLRVKSGHLGDPNGLLANWNESAPNAPCSWTGISCNRKTGQVVAIEFASFGISGRFP ADFCRISTLQKLNLGDNSFGDSISPDSWSLCSHLHFLNISLNFFVGQLPEFIAQFDNLTVLDVNSNNFSGEIPASLVRLPKLQQLNI ANNLLNGSIPEFLTNLTELTRLEIGSNPYKPSPLPSSIGRLSKLQVLFFRYANLVGEIPDSIRDLKSIQNFDAAINNLTGRIPESLG ELKTIQQIELFGNHFSGELPDIFSGLGSLFMFDVSENNLTGKIPESLARLHLISLNLNDNQLEGKIPESLALNPNLCQFKLFNNRFS GTLPQNLGFSDLDEFDVSGNNLEGSLPPNLCSRKKLKTLNLFNNKFNGPIPESYGECNSLAYVRIHDNQFSGELPAGFWGLARYTFL ELRNNNFQGSIPASISNARGLTQLLISGNRFSGELPAEICKLEEVVIMNISKNQLSGELPSCITRLKTLQNLDLSENRITGQIPKSV SSWNDLTELNLANNQLTGEIPGELGTLPVLTYLDLAGNLLSGKIPSELSKLKLNKFNVSNNRLEGKVPLWLDDNYFVSGLRGNPGLC SPDLKPLPECPKPKSVSLYVVCILSAFAFILVGSLVCVLLKASKLLPIRSKHKSVWRITAFQRVGFTERDVLAALTDDNLIGAGGSG RVYRVKLKNGQMVAVKKLWAAKRVRESEEVFRSEVETLGRVRHGNIVKLLYTGIGDDFRILVYEYMENGSLGDVLHGEKIGLLLDWP RRFAIAVGAAQGLAYLHHDCVPAIVHRDVKSNNILLDEDFRPKVADFGLAKAMQQDTEGSDQAMSHVAGSYGYIAPEYAYTLKINEK SDVYSFGVVLLELIIGKRPNDSSFGENKDIVKWVLEGAPSSKKGEGIGHITDGSSILDLNQLVDQRMNPSSSNYTEIKNVFDVALLC TSALPINRPSMRRVVELLKDSSFPRPK
Gene start	143398021
Gene end	143402443
Strand	1

Nicotiana sylvestris IDA-like and *HAE*-like gene families

Gene name	NsylIDA1
SolGenomics source	N.sylvestris Genome
SolGenomics sequence ID	gene_14675 (mRNA_26035)
SolGenomics scaffold	Nsyl_KD945166.1
CDS	ATGGCCTCCTCCTCCTCCTCTTCCTCTTCCTCTTCTTCTTCTAAAAATAAAACCCTTTATTACTTAATTTGTTTGATTCTTGCCATT TCTTTTCTTGTTGGTTATGGAGTTGAAGCAAGACCAGGGAGAATGATAATGGAGGAAGAAGAAGCAAATTCAAGAATATTTTCAACA CAACATTTGAAGGTATACAGAAAAGAGAATGCATACAAAACAGAAAATTTGCTATTTACTATGCTACCAAAAGGGGTTCCAATTCCT CCTTCTGCTCCATCTAAGAGACACAATGCTTTTGTGGACTCTTCTCCTCAAAATTGA
peptide	MASSSSSSSSSSSKNKTLYYLICLILAISFLVGYGVEARPGRMIMEEEEANSRIFSTQHLKVYRKENAYKTENLLFTMLPKGVPIP PSAPSKRHNAFVDSSPQN*
Gene start	74265
Gene end	74582
Strand	1
Gene name	NsylIDA2
SolGenomics source	N.sylvestris Genome
SolGenomics sequence ID	–
SolGenomics scaffold	Nsyl_KD978144.1
CDS	ATGGCTTATTCTACTAACTCTAAAACCTTTCATTTTTCATGGAATTTCATGTGCTTTATTCTTACCCTTTCTCTTGTTCTTGGCTAT GGTGCTGCAGTGAGAACAATGGCGACGGCGACGGCGAGGACGACGACGAAGAAAGAGGAAGCTTCTGGAATGTTCTCAGAGCCTGTG AAAGACTTATATGGTGAAAAGAATGAATATCTGAAAGGTAATTGGTTCAATATGCTACCAAAAGGTGTTCCTATTCCTCCTTCTGCA CCATCCAAAAGGCACAATTATTATGTGAACTCTTACCCTTAA
peptide	MAYSTNSKTFHFSWNFMCFILTLSLVLGYGAAVRTMATATARTTTKKEEASGMFSEPVKDLYGEKNEYLKGNWFNMLPKGVPIPPSA PSKRHNYYVNSYP*
Gene start	88678
Gene end	88980

Strand	-1
Gene name	NsylIDA3
SolGenomics source	N.sylvestris Genome
SolGenomics sequence ID	gene_21416 (mRNA_39345)
SolGenomics scaffold	Nsyl_KD951180.1
CDS	ATGTTGAAAAGGTTTAAAAACACAACAATATTAGTCTTACTACTTTCTCTTCATCTTCTTTTGATTTTCGTGGCTGATTATCACCAT GCAAATGCAACAAAGAACTCACAACTTTTTAATGTTAAGCCTTTGCCTAATTCCCACAATAATTCTCCGCATACATCATTTTCTCAG TCTTTGCCAAAAGGAATCCCTATTCCACCTTCTGCTCCTTCCAAAAGGCACAATGGTATCAACCTCTAA
peptide	MLKRFKNTTILVLLLSLHLLLIFVADYHHANATKNSQLFNVKPLPNSHNNSPHTSFSQSLPKGIPIPPSAPSKRHNGINL*
Gene start	40337
Gene end	40579
Strand	1
Gene name	NsylIDA4
SolGenomics source	N.sylvestris Genome
SolGenomics sequence ID	gene_43020 (mRNA_81453)
SolGenomics scaffold	Nsyl_KD977536.1
CDS	ATGGGGAAAATGAGGACAACACTATTCGTTGTTTTGCTTCTTCTTATGGTTGACCATGCTTATGCTGCAAGGGCAACGCACACACAA TTTCTCAAAGTTCAACCTTTGCATATGATGAATAAATCTCATCAATTCTCAGAGTCTTTGCCAAAAGGGGTCCCAATTCCACCTTCT GCTCCTTCCCAACGGCACAATGGTATCAACCTCAAAAGGCTAATTAGGCCATGA
peptide	MGKMRTTLFVVLLLLMVDHAYAARATHTQFLKVQPLHMMNKSHQFSESLPKGVPIPPSAPSQRHNGINLKRLIRP*
Gene start	13349
Gene end	13576
Strand	1
Gene name	NsylIDA5
SolGenomics source	N.sylvestris Genome
SolGenomics sequence ID	gene_31892 (mRNA_60019)
SolGenomics scaffold	Nsyl_KD962079.1
CDS	ATGATCAGTTTCTTCAGAAGAAAAGTACCTCTTATTCTAGTCTTTTGGATGGCTATTATATTAATCACTATTTTTGGTCATTGTCAT GGCTCAAGAAGCAGCTCTCAAGTATTTAACCCAAGTAGCCACAGAAACTCTCATCAATATGGCCATTTTTGGAATTTAATGCCAAAG AGAATTCCAATACCAGCTTCTGGTCCATCAAGAAAACACAATGATATTGGTCTCAAGAGTACTTGGAGATTACCCTAA
peptide	MISFFRRKVPLILVFWMAIILITIFGHCHGSRSSSQVFNPSSHRNSHQYGHFWNLMPKRIPIPASGPSRKHNDIGLKSTWRLP*
Gene start	38313
Gene end	38564
Strand	1
Gene name	NsylHAE
SolGenomics source	N.sylvestris Genome
SolGenomics sequence ID	gene_41518 (mRNA_78595)
SolGenomics scaffold	Nsyl_KD975002.1
CDS	ATGCAACTATTCATCTTCTTTTTTAGTACTCTGCCTTTGATCTTTGCTTTAAATCAAGATGGGCTATATCTGCAAAGAATGAAGCTT TCTCTTTCCGACACAGAAGGTGCATTTTCTTCTTGGTCTGAACATGACCCTACCCCCTGTAACTGGACAGGTGTCACGTGTAACGAC GCGCCGTCTCCCTCCGTTATCGCCGTTAATCTCTCCGGCGCTTCTCTCGCCGGACCCTTCCCCATTTTCCTCTGCCACCTCCCTTTG CTTTCATCCCTCTCTCTTTCCAATAATCTTATTAACTCTACTCTTCCACTTTCTATTTCTGAATGTCGTAGCCTTACTTACCTTGAC

	CTTTCTCAGAATCTCGTCGGTGGCCCTATTCCTGAAACAATTGCTGATCTGCCTTACCTCAGATACCTTGATCTTAGCGGGTGCTAT TTTACGGGAGATATTCCAGCAAGTTTCGGAAAATTCCAGCAACTGGAGACTCTTATACTTACTGAAAATGTTCTTACTGGTAAAGTT CCTGCTATGTTAGGTAATGTAACGAGTCTCAGGACAATTGAACTCGCTTACAACCCATTTGCACCGAGCCAGTTTCCTCCTGAACTT GGTAACTTGACGAATCTTGAAACATTATGGCTAAGTATGTGTAATCTAGTCGGTTCAATTCCACTTAGTATTGAGAAATTGAGGCGA TTGAGTAATTTTGATGTGTCCAATAATAGACTCGTTGGGCCGATACCAAGTACAATTTTCCAGCTTAATAGTATTGTCCAAATTGAG CTCTATAACAATTCCCTTACTGGATTTTTGCCTAGTGGATGGTCTAACTTGACTAGATTGAGACGATTCGATGTGTCAACTAACAAG TTAAATGGTACTATTCCTGATGAGTTGTGTGAGTTGTCACTTGAGTCACTCAATTTATTTGAGAATCAATTTGAAGGTTTATTTCCA GAAAGTATAGCTAAGTCTCCTAATTTGTATGAGCTCAAGTTATTCTCCAACAGATTTTCAGGGTCACTGCCTAGTGAACTAGGAAAG AACTCAGCTTTACAATATCTTGATGTTTCATACAACAAATTTTCTGGTAAGATTCCAGAAAGTTTGTGTGAAATGGGAGCTTTAGAG GATCTTATTATGATTTACAATTCGTTCTCCGGGAGTATTCCAGCTAGTCTTGGTAACTGTCGGAGTTTGAGACGTGTCAGGTTTCGG GGTAATCAGCTATATGGGGAAGTCCCTACTGAGTTTTGGAGTTTGCCTCAGGTTTATCTTTTAGACCTTTTTGGCAATGCATTTTCA GGGAGTATATCACACATGATTTCTGGTGCCAAAAACTTGTCTAACTTACAAATTTCAAGAAACAGAATATCAGGGGTTATACCTTGT GAAATAGGAAAATTGCAGAATTTAGTTGAGTTTTCCGCGAGTCATAATGAGCTAACGGGAGAAATTCCAGGCACATTAGTACATCTA GGGCAGTTAGGAACCCTTGATCTTAGTTTCAATGAGTTATCAGGCGAAATCCCCTTGGGAATTCACACAATGAAGCAACTCAGTGAG CTTAACCTGGCTAGCAATAGATTTTCGGGAAAAATTCCAGATGAAATTGGGACTTTGCCAGTGCTTAATTATCTTGATCTTTCGGGG AATTACATCTCGGGTGAAATTCCACTCAGTCTGCAAAGCTTGAAGCTTAATAAGCTAAATTTGTCAAATAATCGGCTGTCCGGGACT GTTCCTGCATTTTTTGATAAGGGTGTTTATAGAAATAGCTTTCTAGGAAACCCAAGTTTGTGTCAAGGTGTTGCTGGTCTTTGTACT GCCAAAGGTGGAGGAAAGCGTGAAGGATACTTGTGGGCGTTGAGAGCTATCTACACAGTTGCTGGCTTTGTTTTTCTTGTTGGGATT GCTATGTTCATTTGGAAGTACCAGAAATTCAAGAAAATTAAGAAAGGAATCACTATATCAAAGTGGACATCATTCCATAAGCTCGGA TTCAGTGAATTTGAAATACCTTATGGCCTAGATGAAGCTAATGTAATTGGAAATGGAGCTTCAGGAAGAGTTTACAAAGCTGTCCTT AGCAATGGCGAGGCAGTAGCAGTTAAGAAGCTATGGGAGAGATCAGTTAAAGATGAAACCAGTTTTGGTGCTCTTGAGTCTGATAAA GACGAGTTTGAAATGGAAGTTGAAACTCTGGGAAAAATTAGGCACAAGAATATTGTGAGATTGTGGTGCTGTTGTGATACTGGGGAT AGCAAGCTACTGGTATATGAGTACATGCCGAATGGAAGTTTGGGCGATTTGCTGCACAGTTGCAAGGCCAAATTGTTGGATTGGCCG TTGAGGTTTAAGATAGCTTTAGATGCAGCTGAGGGGCTCTCTTATTTGCACCATGATTGTGTTCCTCCAATTGTTCACCGAGATGTT AAGTCAAACAACATATTACTGGATGGTGAATTTGGAGCAAAAATATCAGATTTTGGTGTGGCAAAAATTGTTAAAGCAGCCAGCAAA GGTGGTGCCGAATCCATGTCTGTAATTGCTGGTTCCTGTGGTTACATTGCACCAGAGTATGCATATACTCTTCATGTGAATGAAAAG AGTGACATTTATAGTTTTGGAGTGGTCATTTTGGAGCTTGTGACAGGACGAAGACCAGTTGGTCCAGAATTTGGAGAGAAAGATCTA GCTACTTGGGTACACACCACCTTGAACGAGAAAGGAGTTGATCAGTTGCTCGACCCAAATATAAATTCCAGCTTCAAAGGACATATA TGCAAAGTTCTTGATATTGGTCTATGTTGTCTTAACCATATTCCAGCTAATCGCCCCTCAATGCGCAGCGTGGTGAAAATGCTCCAA GAATCAGTTCCTTATAATGTGCCAGGGATGGTAGACAAGAATGGTAAATTTTCCCTTAGCTTTTTTCCAAAGTCAGTCCAGTGA
peptide	MQLFIFFFSTLPLIFALNQDGLYLQRMKLSLSDTEGAFSSWSEHDPTPCNWTGVTCNDAPSPSVIAVNLSGASLAGPFPIFLCHLPL LSSLSLSNNLINSTLPLSISECRSLTYLDLSQNLVGGPIPETIADLPYLRYLDLSGCYFTGDIPASFGKFQQLETLILTENVLTGKV PAMLGNVTSLRTIELAYNPFAPSQFPPELGNLTNLETLWLSMCNLVGSIPLSIEKLRRLSNFDVSNNRLVGPIPSTIFQLNSIVQIE LYNNSLTGFLPSGWSNLTRLRRFDVSTNKLNGTIPDELCELSLESLNLFENQFEGLFPESIAKSPNLYELKLFSNRFSGSLPSELGK NSALQYLDVSYNKFSGKIPESLCEMGALEDLIMIYNSFSGSIPASLGNCRSLRRVRFRGNQLYGEVPTEFWSLPQVYLLDLFGNAFS GSISHMISGAKNLSNLQISRNRISGVIPCEIGKLQNLVEFSASHNELTGEIPGTLVHLGQLGTLDLSFNELSGEIPLGIHTMKQLSE LNLASNRFSGKIPDEIGTLPVLNYLDLSGNYISGEIPLSLQSLKLNKLNLSNNRLSGTVPAFFDKGVYRNSFLGNPSLCQGVAGLCT AKGGGKREGYLWALRAIYTVAGFVFLVGIAMFIWKYQKFKKIKKGITISKWTSFHKLGFSEFEIPYGLDEANVIGNGASGRVYKAVL SNGEAVAVKKLWERSVKDETSFGALESDKDEFEMEVETLGKIRHKNIVRLWCCCDTGDSKLLVYEYMPNGSLGDLLHSCKAKLLDWP LRFKIALDAAEGLSYLHHDCVPPIVHRDVKSNNILLDGEFGAKISDFGVAKIVKAASKGGAESMSVIAGSCGYIAPEYAYTLHVNEK SDIYSFGVVILELVTGRRPVGPEFGEKDLATWVHTTLNEKGVDQLLDPNINSSFKGHICKVLDIGLCCLNHIPANRPSMRSVVKMLQ ESVPYNVPGMVDKNGKFSLSFFPKSVQ
Gene start	55601
Gene end	58800
Strand	1
Gene name	NsylHSL1
SolGenomics source	N.sylvestris Genome
SolGenomics sequence ID	gene_9122 (mRNA_15487)
SolGenomics scaffold	Nsyl_KD937107.1
CDS	ATGTTTCTTCAAATCTTTGTTACTCTTTTGTTCCCAACTTTGATTTTCTCACTTAACCAAGAGGGTCTGTATTTACACAACGTGAAG CTCGGATTTGATGACCCTGATAGTGTTCTTTCCAACTGGAATGAGCACGACGAGACACCGTGTAACTGGTTTGGCATAACCTGTGAT CAAACAACTCGGTCCGTTACATCCTTGGACCTCGCCAATGCTAACGTTGCTGGTCCTTTTCCTTCACTTCTCTGTCGGTTGAAGAAA CTGCGTTACATTTCGTTATACAACAACGCTGTTAACTCCACCCTTCCTGAAGATTTTTCCGGGTGTGAATCTTTGGAGCATCTCGAT TTGGCTCAGAATTTGTTGGTCGGTACACTTCCGGCGAGTTTACCTGAGCTTCCGAATTTGAAATACCTTGACTTGGGGGGAAACAAC TTTACCGGCGACATTCCGTCAAGTTTCGGTTCTTTCCGGCAGCTGGAGGTTCTTGGACTGGTTGGGAACTTGCTGGACGGGACTATT CCAGCGTTTCTGGGTAACATTTCGACGTTAAAGCAGCTGAATCTGTCGTACAACCCGTTTTCGACGGGTCAGATCCCGCCGGAGCTG GGAAATCTGACAAATCTCGAGGTTTTGTGGCTCTCGGACTGTAATTTGGTCGGTGAAGTTCCTGATACATTGGGTCGGTTGAAGAAA ATTGTGGATTTGGACCTTGCTGTGAACTACTTGGATGGGCCGATCCCGAGTTGGCTCACTGAGTTAACTAGTGCTGAACAAATTGAG CTGTATAACAACTCGTTCACCGGCGAGTTACCGGCGAATGGGTGGTCGAAAATGACGGCGTTAAGGCGACTCGACGTGTCGATGAAT CGGGTCACGGGTACGGTTCCGAGGGAGTTGTGTGAGTTGCCACTTGAGTCGCTGAATCTGTATGAGAACCAAATGTTTGGTGAATTG CCACAAGGCATTGCGAACTCGCCGAATTTGTACGAGTTGCGGCTTTTTCACAACCGTTTTAATGGTAGTTTGCCTAAAGATCTTGGG AAGAATTCACCTTTGTTGTGGATTGATGTGTCTGAGAATAAATTTTCTGGTGAAATTCCGGAGAATTTGTGTGGGAAAGGGTTTTTG GAAGAGCTTTTGATGATAGATAACGTACTTACTGGTGAAATTCCGGCGAGTTTGAGTGAATGCAGGAGCTTATTGCGGGTGAGATTG GCTCACAATCAATTATCTGGTGATGTTCCGGCGGGTTTCTGGGGCCTACCACACCTTTCCCTGCTTGAGCTCGTGGACAATTCACTA TCTGGTGATATCGCAAAAACTATAGCTAGTGCTTCAAATTTATCAGCTTTGATTTTGTCCAAGAACAAATTTTCAGGTCCCATTCCA

	GAGGAGATTGGTTCTCTGGAAAATCTTCTTGATTTTGTGGGCAACGATAACCAGTTTTCTGGGGCTTTGCCAGCTAGTTTAGTGATG CTGGGGCAATTGGGAAGGCTGGATCTTCACAACAATGAGTTAAATGGTGAGCTTCCAAGTGGGATTCATTCTTTGAAGAGGTTGAAT GAATTGAACTTGGCAAACAATTATCTTTCGGGAGCTATCCCCAAGGAAATTGGGGGCTTGTCTGTTTTGAATTATCTTGATCTATCA GGGAACCAGTTTACAGGGAAGATCCCAATGGAGTTGCAGAATTTGAAGCTTAATCAGCTGAACTTGTCGAACAATGACCTTTCGGGT GATATTCCCCCTTTGTATGCAAAGGAAATGTATAGGAGTAGCTTTTTGGGGAATGCTGGTTTATGTGGAGACATCGAGGGCTTGTGT GAAGGAACAGCTGAAGGTAAAACTGCTGGTTATGTTTGGTTATTGAGGTTACTCTTTACTCTTGCTGGATTGGTGTTTGTAGTTGGG GTGGTTTGGTTCTATTGGAAGTATAAGAATTTTAAGAAAGCTAAAATGGCTATTGATAAGTCTAAATGGACTTTGATGTCGTTTCAT AAGTTGGGTTTCAATGAGTATGAAATCTTGGATGCTCTTGATGAGGACAACTTAATTGGAAGTGGCGCTTCCGGGAAGGTTTACAAG GTTGTTCTGAGCAAGGGTGACACTGTTGCGGTGAAGAAGATTTTGAGAAACACGAAAATAACAGATGAGAGTAGTGATATCGAGAAG GGTAGCATTCAAGATGATGGATTTGAAGCGGAGGTTGAGACATTGGGGAAGATACGGCACAAGAACATTGTTAAGCTATGGTGTTGT TGTACAACAAGGGATTGCAAACTTCTGGTTTACGAGTACATGCCTAATGGAAGCTTGGGTGATTTGCTACACAGCAGCAAAAGCGGC CTTCTAGACTGGCCTATGAGATATAAGATAGCCATGGATGCTGCTGAGGGACTCTCTTACTTGCATCATGACTGTGCTCCGCCGATT GTTCACAGAGATGTTAAGTCAAACAACATCTTGTTGGATGGTGATTTTGGAGCTCGAGTTGCTGATTTTGGTGTAGCGAAGGCGGTC GATGCCAATGCCAAGGGAATCAAGTCCATGTCTGTCATTGCAGGGTCTTGTGGTTACATTGCTCCAGAATATGCATATACACTGCGG GTGAACGAGAAGAGCGATACATACAGCTTCGGTGTGGTAATCCTAGAGCTTGTGACTGGGAAGCGCCCTGTGGATCCCGAATTCGGG GAAAAGGATTTGGTGAAGTGGGTATGCTCTACACTGGACCAGAAGGGTGTAGATCATGTAATTGACCCTAAACATGATTCTTGTTTC AAGGAGGAGATATGCAAGGTCTTAAATATTGGCCTCCTCTGCACTAGCCCTCTCCCAATCAACCGACCCTCGATGAGACGGGTCGTA AAAATGTTGCAAGAAGTGGGTGCTGGGAACCTGCCCAAGGCTGCTTCTAAGGATGGCAAATTGACTCCTTATTACTATGAAGAAGCA TCAGATCAAGGAAGTGTAGCTTAA
peptide	MFLQIFVTLLFPTLIFSLNQEGLYLHNVKLGFDDPDSVLSNWNEHDETPCNWFGITCDQTTRSVTSLDLANANVAGPFPSLLCRLKK LRYISLYNNAVNSTLPEDFSGCESLEHLDLAQNLLVGTLPASLPELPNLKYLDLGGNNFTGDIPSSFGSFRQLEVLGLVGNLLDGTI PAFLGNISTLKQLNLSYNPFSTGQIPPELGNLTNLEVLWLSDCNLVGEVPDTLGRLKKIVDLDLAVNYLDGPIPSWLTELTSAEQIE LYNNSFTGELPANGWSKMTALRRLDVSMNRVTGTVPRELCELPLESLNLYENQMFGELPQGIANSPNLYELRLFHNRFNGSLPKDLG KNSPLLWIDVSENKFSGEIPENLCGKGFLEELLMIDNVLTGEIPASLSECRSLLRVRLAHNQLSGDVPAGFWGLPHLSLLELVDNSL SGDIAKTIASASNLSALILSKNKFSGPIPEEIGSLENLLDFVGNDNQFSGALPASLVMLGQLGRLDLHNNELNGELPSGIHSLKRLN ELNLANNYLSGAIPKEIGGLSVLNYLDLSGNQFTGKIPMELQNLKLNQLNLSNNDLSGDIPPLYAKEMYRSSFLGNAGLCGDIEGLC EGTAEGKTAGYVWLLRLLFTLAGLVFVVGVVWFYWKYKNFKKAKMAIDKSKWTLMSFHKLGFNEYEILDALDEDNLIGSGASGKVYK VVLSKGDTVAVKKILRNTKITDESSDIEKGSIQDDGFEAEVETLGKIRHKNIVKLWCCCTTRDCKLLVYEYMPNGSLGDLLHSSKSG LLDWPMRYKIAMDAAEGLSYLHHDCAPPIVHRDVKSNNILLDGDFGARVADFGVAKAVDANAKGIKSMSVIAGSCGYIAPEYAYTLR VNEKSDTYSFGVVILELVTGKRPVDPEFGEKDLVKWVCSTLDQKGVDHVIDPKHDSCFKEEICKVLNIGLLCTSPLPINRPSMRRVV KMLQEVGAGNLPKAASKDGKLTPYYYEEASDQGSVA
Gene start	9901
Gene end	13300
Strand	1
Gene name	NsylHSL2
SolGenomics source	N.sylvestris Genome
SolGenomics sequence ID	gene_27949 (mRNA_52300)
SolGenomics scaffold	Nsyl_KD957655.1
CDS	ATGGAACACACGAAACTCCAATTTCTGCTACTCATACAACTGTTTCTATTCATTATTCCGGCTAGTTGCTTGAACCGCGATATCGCC ATTTTACTCCGGGTTAAGACAGGTCAGCTCGGTGACCCCAATGGATTGCTCTCTGATTGGAACGCGTCTGCTCCAAATGCGCCTTGT AACTGGACCGGCATTACCTGTGATCGTAAAACGCATAAGGTTGTCTCCATCGAGTTCACCAGTTTTGGAATCTCAGGTCATTTTCCG GCCGACTTCTGCCGGATTTCGACTTTGCAGAAACTCAATCTGGGCGATAACAGTTTCGGTGACTCTATTTCCTCTGACTCCTGGTCC CTATGTTCGCATCTGCACTTTTTGAATCTTTCTTTAAATTTCTTCGTTGGCAAGCTGCCGGAGTTTATAGCCAAGTTTGATAACTTG ACCGTGCTTGATGTTAATTCAAACAATTTCTCCGGTGATATTCCGGCGAGCTTAGGCCGGTTACCGAGATTACAAGAGCTCGATATT GCCAACAATCTCCTTAATGGTTCAGTTCCTGAGTTCTTATCCAATCTCACCGAGTTGACTCGATTGGTCATTGCTCAAAATCCATTT AAGCCAAGTCCATTGCCTTCCTCAATTGGACGACTAGGTAAACTTCGAATTCTATATGCTCGGTTTGCGAATCTTATTGGAAATATT CCAGATTCCATTAAAGACCTGAAATCTATTCAGAATTTTGACGTGGCGATTAACAATCTAACTGGAAAAATTCCAGAAAGCATTGGA GAGCTGAAAACCGTAGAACAAATAGAGCTCTTTCAGAATAAATTTTCAGGTGAACTGCCGAACACGTTTTCGGGACTTGTTTCTCTG TTCAGGTTTGACGCTTCTCAGAATAATCTCACGGGAAAAATACCTGATAGCCTTGCCCGTTTGCCGCTGGTATCTTTGAATCTCAAT GATAACAATTTAGAAGGCGAAATTCCAGAAAGTTTAGCTCTTAACCCGAATCTTACTCAGTTCAAGCTCTTTAACAACAAATTTTCA GGTACTTTACCTCAAGATTTTGGTATGAGTTCAGATTTGGATGAGTTTGATGTCTCTGGCAATAATCTCGAAGGTTCTTTGCCCCCC AATTTATGTTCCAGAAAGAAACTTAGGATTTTGAACCTGTTCGATAATAGGTTCAGTGGTTCAGTCCCTGAATCCTATGGGGAGTGT AATTCACTAACGTACGTGCGTATCTATAACAACCAATTCTCTGGTGAATTACCAACTGGTTTCTGGAGTTTTGCTGGATACACATTT CTTGAACTGAGAAACAACAACTTTCAAGGTTCAATTCCAGCTTCAATCTCCAATGCTCGTGGCCTAACAGAAATTCTCATCTCCGGT AACAAATTCTCCGAGGAATTGCCGGCGGGATTATGCAATTTGGAAGAGATTGTGATTATGGACATAAGCAAGAATCAATTATCAGGA GATTTGCCTTCATGTATCACAAAGATGAAAACGTTACAAAAGCTTGATCTTTCAGAAAATAGGATCACGGGTCAAATTCCCAAATTA GTTAGTTCTTGGACCGACTTGACTGAACTGAATTTAGCTAACAATCAATTGACAGGTGAAATTCCAGGTGAGCTTGGGACTTTGCCG GTTTTGACGTACTTAGACCTCGCTGGAAACTCGCTTTCCGGCGAAATTCCGTCGGAGCTGAGCAACCTCAAGCTTAACAAGTTCAAC GTATCAAATAACAGGCTTGAAGGAAAAGTGCCACTTGTGTTTGATAATGATTTTTTCATCTCGGGTTTGCAGGGCAATCCGGATCTT TGTAGTCCGGATCTTAAACCTCTACCTCAGTGCCCAAGACCCAAAAGTATTAGCTTGTATTTGGTGTGTATTTTATCAGCTTTATCC GTCATACTTGTCGGGTCACTTGTTTGGGTCTTGATCAAGGCCAAAAAGTTGCTACCCATTCGGAGTAAGCGTAAAAGTGCATGGAGA ATTACTGCATTTCAACGGGTTGGATTCACGGAGGGAGACTTGTTAGCTTCACTGACAAATGAGAATCTCATTGGAGCTGGTGGGTCT GGTCGGGTATATAGGGTCAAACTGAAAAACGGGCAGATGGTCGCGGTTAAGAAGCTTTGGGAGGCTAAACGGGAGAGAGAATCTGAG GAGGTTTTCAGGTCGGAGGTGGAGACTCTAGGGAGAGTCCGACATGGAAACATAGTAAAACTATTGTACAGTGGCATTGGTGACGAC TTCAGGATATTGGTGTATGAGTACATGGAAAATGGGAGCTTAGGAGATGTATTACATGGGGAAAAAGGTGGCATTCTTTTGGATTGG

	CCAAGGAGATTTGGCATAGCAGTTGGAGCAGCTCAAGGATTGGCCTATTTGCACCATGATTCTGTTCCTGCAATAGTGCACAGAGAT GTCAAGTCTAATAACATTTTGTTGGACGAGGATTTTAGGCCAAAAGTTGCTGATTTTGGGCTAGCTAAGGTAATGCAGCAGGACAGT GAGGAGAGTGATCAAGTCATGTCCCATATTGCTGGTTCCTACGGCTACATTGCACCTGAATATGCGTATACTCTGAAGATTAATGAG AAGAGTGACGTTTATAGCTTTGGTGTGGTACTGTTGGAACTAATAACCGGTAAAAGGCCCAATGACTCCTCTTTCGGTGAGAACAAG GACATGGTCAAGTGGGTGTTAGAGGTTGCAATATCGTCTAAAAAAGATGAAGGAAGTGGCCGTGTCACGGGCAGCAATAGTATTCTT GATTTGAACCAGCTAGTCGACCAGAGAATGAATCCGTCTGCAAGCAATTATGCAGAGATTAAAAAGGTTTTTGATGTGGCTTTGCTT TGCACTTCTTCATTGCCCATTAACAGGCCGTCCATGAGAAGAGTTGTTGAATTGTTGAAGGATAACAGTGTTGCTCGTTCTAAGTCA ATCCGATAG
peptide	MEHTKLQFLLLIQLFLFIIPASCLNRDIAILLRVKTGQLGDPNGLLSDWNASAPNAPCNWTGITCDRKTHKVVSIEFTSFGISGHFP ADFCRISTLQKLNLGDNSFGDSISSDSWSLCSHLHFLNLSLNFFVGKLPEFIAKFDNLTVLDVNSNNFSGDIPASLGRLPRLQELDI ANNLLNGSVPEFLSNLTELTRLVIAQNPFKPSPLPSSIGRLGKLRILYARFANLIGNIPDSIKDLKSIQNFDVAINNLTGKIPESIG ELKTVEQIELFQNKFSGELPNTFSGLVSLFRFDASQNNLTGKIPDSLARLPLVSLNLNDNNLEGEIPESLALNPNLTQFKLFNNKFS GTLPQDFGMSSDLDEFDVSGNNLEGSLPPNLCSRKKLRILNLFDNRFSGSVPESYGECNSLTYVRIYNNQFSGELPTGFWSFAGYTF LELRNNNFQGSIPASISNARGLTEILISGNKFSEELPAGLCNLEEIVIMDISKNQLSGDLPSCITKMKTLQKLDLSENRITGQIPKL VSSWTDLTELNLANNQLTGEIPGELGTLPVLTYLDLAGNSLSGEIPSELSNLKLNKFNVSNNRLEGKVPLVFDNDFFISGLQGNPDL CSPDLKPLPQCPRPKSISLYLVCILSALSVILVGSLVWVLIKAKKLLPIRSKRKSAWRITAFQRVGFTEGDLLASLTNENLIGAGGS GRVYRVKLKNGQMVAVKKLWEAKRERESEEVFRSEVETLGRVRHGNIVKLLYSGIGDDFRILVYEYMENGSLGDVLHGEKGGILLDW PRRFGIAVGAAQGLAYLHHDSVPAIVHRDVKSNNILLDEDFRPKVADFGLAKVMQQDSEESDQVMSHIAGSYGYIAPEYAYTLKINE KSDVYSFGVVLLELITGKRPNDSSFGENKDMVKWVLEVAISSKKDEGSGRVTGSNSILDLNQLVDQRMNPSASNYAEIKKVFDVALL CTSSLPINRPSMRRVVELLKDNSVARSKSIR
Gene start	30001
Gene end	33700
Strand	-1

Nicotiana tomentosiformis IDA-like and *HAE*-like gene families

Gene name	NtomIDA1
SolGenomics source	N.tomentosiformis Genome
SolGenomics sequence ID	gene_42689 (mRNA_79074)
SolGenomics scaffold	Ntom_KB972926.1
CDS	ATGGCCTCCTCCTCCTCCTCTTCCTCTTCTTCTTCTAAAAATAAAACTCTTTATTACTTAATTTGTTTGATTCTTGCCATTTCTTTT CTTCTTGGTTATGGAGTCGAAGCAAGACCAATCGAAGAAGCTAATTCAAGAATATTTTCATCACAACATTTGAAGGTATACAGAAAA GAGAATGCATACAAAACAGAAAATTTGCTATTTACTATGCTACCAAAAGGGGTTCCAATTCCTCCTTCTGCTCCATCCAAAAGGCAC AATGCTGTTATGGACTCTTCACCTCAAAATTGA
peptide	MASSSSSSSSSKNKTLYYLICLILAISFLLGYGVEARPIEEANSRIFSSQHLKVYRKENAYKTENLLFTMLPKGVPIPPSAPSKRH NAVMDSSPQN*
Gene start	26032
Gene end	26325
Strand	1
Gene name	NtomIDA2
SolGenomics source	N.tomentosiformis Genome
SolGenomics sequence ID	–
SolGenomics scaffold	Ntom_KB954314.1
CDS	ATGGCTTATTCTACTAATTCTAAAACCTTTCATTTTTCATGGAATTTCATTTGCTTGATTCTTACCCTTTCTCTTGTTCTTGGCTAT GGTGCTGCAGTGAGAACAATGGCGACAACGACGACGACGAAAGAGGAAGCTTCTGGAATGTTCTCAGAGCCTGTGAAAAACTTATAT AGTGAAAAGAAAGAATTTCTGAAAGGTAATTGGTTCAATATGCTACCAAAAGGTGTTCCTATTCCTCCTTCTGCACCATCCAAAAGG CACAATTATTATGTGAACTCTTACCCTTAA
peptide	MAYSTNSKTFHFSWNFICLILTLSLVLGYGAAVRTMATTTTTKEEASGMFSEPVKNLYSEKKEFLKGNWFNMLPKGVPIPPSAPSKR HNYYVNSYP*
Gene start	53025
Gene end	53614
Strand	1
Gene name	NtomIDA3
SolGenomics source	N.tomentosiformis Genome

SolGenomics sequence ID	gene_38486 (mRNA_71046)
SolGenomics scaffold	Ntom_KB969023.1
CDS	ATGTTGAAAAGGATTAAAAACACAACAATATTAGTCTTGCTACTTTTTCTTCTTCTTCTTATCTTTATGGCTGATAATCACCATGCA AATGCAGCAAAGAACTCACAACTTTTTAATGTTAAGCCATTGACTAATTCCCACAATAATTCTCCTCACAAATCATTTTCTCAGTCT TTGCCAAAAGGAATCCCTATTCCACCTTCTGCTCCTTCCAAAAGGCACAATGGTATCAACCTCTAA
peptide	MLKRIKNTTILVLLLFLLLLIFMADNHHANAAKNSQLFNVKPLTNSHNNSPHKSFSQSLPKGIPIPPSAPSKRHNGINL*
Gene start	33965
Gene end	34204
Strand	1
Gene name	NtomIDA4
SolGenomics source	N.tomentosiformis Genome
SolGenomics sequence ID	gene_21697 (mRNA_38310)
SolGenomics scaffold	Ntom_KB956501.1
CDS	ATGGGGAAAATGAGGACAATACTATTCGTTGTTTTGCTTCTTCTGATCGTTGGCCAGGTTTATGCTGCAAGGCACACACAATTTCTC AAAGTTAAGCCTTTGCATATTAATAAATCTCAATTCTCAGAGTCTTTGCCAAAAGGGGTTCCAATTCCACCTTCTGCTCCTTCCCAA AGGCACAATGGTATCAACCTCAAACAGCTTCGGCCATGA
peptide	MGKMRTILFVVLLLLIVGQVYAARHTQFLKVKPLHINKSQFSESLPKGVPIPPSAPSQRHNGINLKQLRP*
Gene start	19193
Gene end	19405
Strand	-1
Gene name	NtomIDA5
SolGenomics source	N.tomentosiformis Genome
SolGenomics sequence ID	gene_25187(mRNA_45138)
SolGenomics scaffold	Ntom_KB958630.1
CDS	ATGATCAGTTTCTTCAGAAGAAAAGTACCTCTTATTCTAGTCTTTTGGATGGCTATTATATTAATCACTATTTTTGGTCATTGTCAT GGCTCAAGAACCAGCTCTCAAGTATTTAACCCAAGTAGCCAAAGAAACTCTCATAAATATGGCCATTTTTGGAACTTATTGCCAAAG AGAATTCCAATACCAGCTTCTGGTCCATCAAGAAAACACAATGATATTGGTCTTAAGAGTACTTGGAGATTTCCCTGA
peptide	MISFFRRKVPLILVFWMAIILITIFGHCHGSRTSSQVFNPSSQRNSHKYGHFWNLLPKRIPIPASGPSRKHNDIGLKSTWRFP*
Gene start	30910
Gene end	31161
Strand	-1
Gene name	NtomHAE
SolGenomics source	N.tomentosiformis Genome
SolGenomics sequence ID	gene_37857 (mRNA_69761)
SolGenomics scaffold	Ntom_KB968468.1
CDS	ATGTTAGGTAATGTAACGAGTCTCAGGACAATTGAACTCGCTTACAACCCATTTGCACCGAGCCAGTTTCCTCCTGAACTTGGTAAC TTGACGAATCTTGAGACATTATGGCTAAGTATGTGTAATCTTGTTGGTTCACTTCCACTTAATATTGAGAAATTGAGTCGATTGACT AATTTTGATGTGTCCAATAATAGACTCGTTGGGTCAATACCAAGTACAATTTTCCAGCTTAATAGTATTGTCCAAATTGAGCTATAC AATAATTCCCTTACTGGATTTTTGCCTAGTGGATGGTCTAACTTGACTAGATTGAGACGATTCGATGTGTCAACTAACAAGTTAAAT GGAACAATTCCTGATGAGTTGTGTGAGTTGTCACTTGAGTCACTCAATTTATTTGAGAATCAATTTGAAGGTTTATTTCCAGAAAGT ATAGCTAAGTCTGCTAATTTGTATGAGCTCAAGTTATTCTCTAACAGATTTTCAGGGTCATTGCCTAGTGAACTAGGAAAGAACTCT GCTTTACAGTATCTTGATGTTTCGTACAACAAATTTTCTGGTAAGATTCCAGAAAGTTTGTGTGAAATGGGAGCTTTAGAGGATCTT ATTATGATTTACAATTCGTTCTCCGGGAGTATTCCAGCTAGTCTTGGTAACTGTCGGAGTTTGAGACGTGTCAGGTTTAGGGGTAAT CAGCTATATGGGGAAGTCCCTACTGAGTTTTGGAGTTTGCCTCAGGTTTATCTTTTAGACCTTTTTGGCAATGCATTTTCAGGAAAT ATATCACACATGATTTCTGGTGCCAAAAATATGTCTAACCTGCAAATATCAAGAAACAAACTCTCAGGGGTTATACCTAGTGAAGTA GGAAAATTGAAGAATTTAGTTGAGTTTTCCGCGAGTCATAATGAGCTAACGGGAGAAATTCCAGGCACATTAGTGCATCTAGGTCAG

	TTAGGAACCCTTGATCTTAGTTTCAATGAGTTATCAGGGGAAATCCCCTTGGGAATTCACACAATGAAGCAACTCAGTGAGCTTAAC TTGGCTAACAATGGGTTTTCGGGGAAAATTCCAGAAGAAATTGGGACTTTGCCAGTGCTTAATTATCTTGATCTTTCTGGGAATTAC TTCTCGGGTGAAATCCCACTCAGTCTGCAAAGCTTGAAGCTTAATAAGCTAAATTTGTCTAATAATCGTCTGTCGGGGACTGTTCCT GCATTTTTCGATAAGGGTGTTTACAGCAATAGCTTTCTAGGAAACCCAAGTTTGTGTCAAGGTGTTGCTGGTCTTTGTACTGCTAAA AGTGGAGGAAATCGTGAACGATATTTGTGGGTGTTGAGAGCTATCTATACAATTGCTGGCTTTGTTTTTCTTGTTGGGATTGCTATG TTCATTTGGAGGTACCAGAAATTCAAGAAAATTAAGAAAGGAATCACTATATCAAAGTGGACATCATTCCATAAACTCGGATTCAGT GAACTCGAAATACCTGATGGACTAGATGAAGCTAATGTAATTGGAAATGGAGCTTCGGGAAGAGTTTACAAAGCTGTCTTAAGCAAT GGTGAGGCAGTAGCAGTTAAGAAGCTATGGGAAAGATCAGTTAAAGATGAAACCGGTTTTGGTGCACTTGAGTCTGATAAAGATGAG TTTGAAATGGAAGTTGAAACTCTGGGTAAAATTAGGCACAAGAATATTGTTAGATTGTGGTGCTGTTGTGATACTGGGGATAGCAAG CTCTTGGTATATGAGTACATGCCGAATGGAAGTTTGGGCGATTTGCTGCACAGTTGCAAAGCCAAATTGTTGGATTGGCCGTTGAGA TTCAAGATAGCTTTAGATGCAGCTGAGGGACTCTCTTATTTGCACCATGATTGTGTTCCTCCAATTGTTCACCGAGATGTTAAGTCA AACAACATATTACTGGATGGTGAGTTTGGCGCCAAAATTTCAGATTTTGGTGTGGCGAAAATTGTTAAAGCAGCCAGCAAAGGTGGT GCCGAATCCATGTCCGTAATTGCTGGTTCCTGTGGTTACATTGCACCAGAGTATGCATATACTCTTCATGTGAATGAAAAGAGCGAT ATTTATAGCTTTGGAGTGGTCATCTTGGAGCTGGTGACAGGCAGAAGACCAGTTGGTCCAGAATTTGGGGAGAAAGATCTAGCTACT TGGGTACGCACCACCTTGAACGAGAAAGGAGTTGATCAGTTGCTCGACCCAAATTTAAATTCCACCTTCAAAGAACATATATGCAAA GTTCTTGATATTGGTCTATGTTGTCTTAACCATATTCCAGCTAATCGCCCCTCAATGCGCAGAGTTGTGAAAATGCTCCAAGAATCA GTTCCTTATAATGTGCCAGGGATGGTAAACAAGAATGGTAAACTTCTCCCTTACTTTTTTCCAAAGTCAGTCTAG
peptide	MLGNVTSLRTIELAYNPFAPSQFPPELGNLTNLETLWLSMCNLVGSLPLNIEKLSRLTNFDVSNNRLVGSIPSTIFQLNSIVQIELY NNSLTGFLPSGWSNLTRLRRFDVSTNKLNGTIPDELCELSLESLNLFENQFEGLFPESIAKSANLYELKLFSNRFSGSLPSELGKNS ALQYLDVSYNKFSGKIPESLCEMGALEDLIMIYNSFSGSIPASLGNCRSLRRVRFRGNQLYGEVPTEFWSLPQVYLLDLFGNAFSGN ISHMISGAKNMSNLQISRNKLSGVIPSEVGKLKNLVEFSASHNELTGEIPGTLVHLGQLGTLDLSFNELSGEIPLGIHTMKQLSELN LANNGFSGKIPEEIGTLPVLNYLDLSGNYFSGEIPLSLQSLKLNKLNLSNNRLSGTVPAFFDKGVYSNSFLGNPSLCQGVAGLCTAK SGGNRERYLWVLRAIYTIAGFVFLVGIAMFIWRYQKFKKIKKGITISKWTSFHKLGFSELEIPDGLDEANVIGNGASGRVYKAVLSN GEAVAVKKLWERSVKDETGFGALESDKDEFEMEVETLGKIRHKNIVRLWCCCDTGDSKLLVYEYMPNGSLGDLLHSCKAKLLDWPLR FKIALDAAEGLSYLHHDCVPPIVHRDVKSNNILLDGEFGAKISDFGVAKIVKAASKGGAESMSVIAGSCGYIAPEYAYTLHVNEKSD IYSFGVVILELVTGRRPVGPEFGEKDLATWVRTTLNEKGVDQLLDPNLNSTFKEHICKVLDIGLCCLNHIPANRPSMRRVVKMLQES VPYNVPGMVNKNGKLLPYFFPKSV
Gene start	8101
Gene end	11200
Strand	-1
Gene name	NtomHSL1
SolGenomics source	N.tomentosiformis Genome
SolGenomics sequence ID	gene_25251 (mRNA_45251)
SolGenomics scaffold	Ntom_KB958681.1
CDS	ATGTTTCTTCAAATCTTTGTTACCCTTTTGTTCCCAACTTTGATTTTCTCACTTAACCAAGAGGGTCTGTATTTGCACAACGTGAAG CTCGGATTTGATGACCCTGATAATGTTCTTTCCAACTGGAATGAACACGACGAGACACCATGTAACTGGTTTGGCATAACATGTGAC AAAACAACTCGGTCTGTTACGTCCTTAGACCTCGCTAATGCTAACGTTGCTGGTCCTTTTCCTTCACTTCTCTGTCGGTTAAAAAAA CTCCGTTACATTTCGTTATACAACAACGCCGTTAACTCCACTCTTCCTGAAGATTTCTCCGGGTGTGAATCTTTGGAGCATCTCGAT TTGGCTCAGAATTTTTTGGTCGGTACACTTCCGGCGAGTTTACCTGCGCTTCCAAATTTGAAATACCTGGACTTGTCGGGAAACAAC TTTACTGGCGACATTCCGGCGAGTTTCGGTTCTTTCCGGCAGCTGGAGGTTCTTGGACTGGTTGGGAACTTGCTTGACGGGACTATT CCGGCGTTTCTGGGTAACATTTCAACGTTAAAGCAGCTGAATCTGTCGTACAACCCGTTTTCGACGGGTCGGATCCCGCCGGAGCTG GGTAATCTGACTAATCTCGAGGTTTTGTGGCTTTCCGACTGTAATTTGGTCGGTGAAGTTCCTGATACATTGGGTCGGTTGAAGAAT ATTGTGGATTTGGACCTTGCTGTGAACTACTTGGATGGGCCGATCCCGAGTTGGCTCACTGAGTTAACTAATGCTGAACAAATTGAG CTGTATAACAACTCGTTCACCGGCGAGTTACCGGTGAATGGGTGGTCGAAAATGACAGCGTTAAGGCGACTCGACGTGTCGATGAAT CGGGTCACGGGTACGGTTCCGAGGGAGTTGTGTGAGTTGCCACTTGAGTCACTGAATCTTTATGAGAACCAAATGTTCGGTGAATTG CCACAAGGCATTGCGAATTCGCCGAATTTGTATGAGTTGCGGCTTTTTCACAACCGTTTTAATGGTAGTTTGCCTAAAGATCTCGGG AAGAATTCACCTTTGTTGTGGATTGATGTGTCTGAAAATAAATTTTCCGGCGAACTTCCGGAGAATTTGTGTGGGAAAGGGTTTTTG GAGGAGCTTTTGATGATAGATAACTTACTTACCGGTGAAATTCCGGCGAGTTTGAGTGAATGCCGGAGCTTACTGCGGGTGAGATTG GCTCACAATCAGTTCTCTGGTGATGTTCCGGCGGGATTCTGGGGCCTACCACACCTTTCCCTGCTTGAGCTCATGGACAATTCACTG TCTGGTGATATCGCAAAAACTATAGCTAGTGCTTCAAATTTATCAGCTTTGATTTTGTCCAAGAACAAATTTTCAGGTCCTATTCCG GAGGAGATTGGTTCTCTGGAAAATCTTCTTGATTTTGTGGGCAATGATAACCTGTTTTCTGGGCCTTTGCCAGCTAGTTTAGTGATG CTTGGACAATTGGGAAGGCTGGATCTTCACAATAATGAGTTAATTGGTGAGCTTCCAAGTGGGATTCATTCTTTGAAGAAGTTGAAT GAATTGAACTTGGCAAATAATGATCTTTCTGGAGCTATCCCCAAGGAAATTGGGAGCTTGTCTGTTTTGAATTATCTTGATCTATCG GGAAACCAGTTTTCAGGGAAGATCCCAATGGAGTTGCAGAATTTGAAGCTCAATCAGCTGAACTTGTCGAACAATGATCTTTCGGGT GATATCCCCCCGTTGTATGCAAAGGAAATGTACAAGAGTAGCTTTTTCGGGAACGCTGGTTTATGTGGAGACATTGAGGGCTTGTGT GAAGGAACAGCTGAAGGTAAAACTGCTGGTTATGTTTGGTTATTAAGGTTACTCTTTACTCTTGCTGGATTGGTGTTTGTAGTTGGG GTTGTTTGGTTCTATTGGAAGTATAAGAATTTTAAGAAAGCTAATATGGCTATTGATAAGTCTAAATGGACTTTGATGTCGTTTCAT AAGTTGGGTTTCAATGAGTATGAAATACTGGATGCTCTTGATGAGGACAACTTAATTGGAAGTGGCGCTTCGGGGAAGGTTTACAAG GTTGTTCTGAGCAAGGGTGACACTGTTGCGGTGAAGAAGATTTTGAGAAGTGCGAAAATAACAGATGATAGTAGTGATATCGAGAAG GGTAGCATTCAAGATGATGGATTTGAAGCAGAGGTTGAGACATTGGGGAAGATTCGGCACAAGAACATTGTTAAGCTATGGTGTTGT TGTACAACAAGGGATTGCAAACTTCTGGTTTACGAGTACATGCCTAATGGAAGCTTGGGTGATTTGCTACACAGCAGCAAAAGTGGC CTTCTAGACTGGCCTATGAGATATAAGATAGCCATGGATGCTGCGGAGGGACTCTCTTACTTGCATCATGACTGTGCTCCGCCGATT GTTCACAGAGATGTTAAGTCAAACAACATCTTGTTGGATGGTGATTTTGGAGCTCGAGTTGCTGATTTTGGTGTAGCAAAGGCGGTC GATGCCAATGCCAAGGGAATCAAGTCCATGTCTGTCATTGCAGGGTCTTGTGGTTACATTGCTCCAGAATATGCATACACACTGCGG GTGAATGAGAAGAGCGATATATACAGCTTCGGTGTGGTAATCCTAGAGCTTGTGACTGGGAAGCGCCCCGTGGATCCCGAGTTTGGG

	GAAAAGGATTTGGTGAAGTGGGTATGCTCTACACTGGACCAGAAGGGTGTAGATCATGTAATTGACCCTAAACATGATTCTTGTTTC AAAGAGGAGATATGCAAGGTCTTAAATATTGGCCTCCTCTGCACTAGCCCTCTCCCAATCAACCGACCCTCGATGAGACGGGTCGTA AAAATGTTGCAAGAAGTGGGTGCTGGGAACCTGCCCAAGGCTGCTTCTAAGGATGGCAAATTGACTCCTTATTACTATGAAGAAGCA TCAGATCAAGGAAGTGTAGCTTAA
peptide	MFLQIFVTLLFPTLIFSLNQEGLYLHNVKLGFDDPDNVLSNWNEHDETPCNWFGITCDKTTRSVTSLDLANANVAGPFPSLLCRLKK LRYISLYNNAVNSTLPEDFSGCESLEHLDLAQNFLVGTLPASLPALPNLKYLDLSGNNFTGDIPASFGSFRQLEVLGLVGNLLDGTI PAFLGNISTLKQLNLSYNPFSTGRIPPELGNLTNLEVLWLSDCNLVGEVPDTLGRLKNIVDLDLAVNYLDGPIPSWLTELTNAEQIE LYNNSFTGELPVNGWSKMTALRRLDVSMNRVTGTVPRELCELPLESLNLYENQMFGELPQGIANSPNLYELRLFHNRFNGSLPKDLG KNSPLLWIDVSENKFSGELPENLCGKGFLEELLMIDNLLTGEIPASLSECRSLLRVRLAHNQFSGDVPAGFWGLPHLSLLELMDNSL SGDIAKTIASASNLSALILSKNKFSGPIPEEIGSLENLLDFVGNDNLFSGPLPASLVMLGQLGRLDLHNNELIGELPSGIHSLKKLN ELNLANNDLSGAIPKEIGSLSVLNYLDLSGNQFSGKIPMELQNLKLNQLNLSNNDLSGDIPPLYAKEMYKSSFFGNAGLCGDIEGLC EGTAEGKTAGYVWLLRLLFTLAGLVFVVGVVWFYWKYKNFKKANMAIDKSKWTLMSFHKLGFNEYEILDALDEDNLIGSGASGKVYK VVLSKGDTVAVKKILRSAKITDDSSDIEKGSIQDDGFEAEVETLGKIRHKNIVKLWCCCTTRDCKLLVYEYMPNGSLGDLLHSSKSG LLDWPMRYKIAMDAAEGLSYLHHDCAPPIVHRDVKSNNILLDGDFGARVADFGVAKAVDANAKGIKSMSVIAGSCGYIAPEYAYTLR VNEKSDIYSFGVVILELVTGKRPVDPEFGEKDLVKWVCSTLDQKGVDHVIDPKHDSCFKEEICKVLNIGLLCTSPLPINRPSMRRVV KMLQEVGAGNLPKAASKDGKLTPYYYEEASDQGSVA
Gene start	11701
Gene end	15400
Strand	1
Gene name	NtomHSL2
SolGenomics source	N.tomentosiformis Genome
SolGenomics sequence ID	gene_23142 (mRNA_41082)
SolGenomics scaffold	Ntom_KB957417.1
CDS	ATGGAACACATGAAACTCCAATTTCTGCTACTCATACAACTGTTTTTATTCATTATTCCGGCGAGTTGCTTGAACCGCGATATTGCC ATTTTACTCCGGGTTAAAACTGGTCAGCTCGGTGACCCCAATGGGTTGCTCTCTGATTGGAACGCATCAGCTCCAAATGCGCCTTGT AACTGGACTGGCATTACCTGTGATCGTAAAACGCGTAAGGTTGTCTCCATCGAGTTCACCAGTTTTGGAATCTCCGGTCATTTTCCG GCCGACTTTTGCCGGATTTCGACTTTGAAGAAACTCAATGTCGGCGATAACAGTTTCGGTGACTCTATTTCCTCCGACTCCTGGTCT CTATGTTCGCATCTGCACTTTTTGAATCTTTCTTTAAATTTCTTCGTTGGCAAGCTACCGGAGTTTATAGCCAAGTTTGATAACTTG ACCGTCCTTGATGTTAATTCAAACAATTTCTCCGGTGATATTCCGGCGAGCTTAGGCCGGTTACCGAGATTACAAGAGCTCGATATT GCCAACAATCTCCTTAATGGTTCAGTTCCTGAGTTCTTATCCAATCTTACCGAGTTGACTCGATTGGTCATTGCTCAAAATCCATTT AAGCCAAGTCCATTGCCTTCCTCAATCGGACGACTAGGTAAACTTCGAATTCTATATGCTCGGTTTGCGAATCTTATTGGAAATATT CCAGATTCCATTAAGGACCTGAAATCTATTCAGAATTTTGACGTGGCAATCAACAATCTTACTGGAAAAATTCCAGAAATCATTGGA GAACTGAAAACCGTAGAACAAATAGAGCTTTTTCAGAATAAATTTTCAGGTGAATTGCCGAACACGTTTTCGGGACTTGTTTCTCTG TTCAGGTTTGACGCTTCTCAGAACAATCTCACGGGAAAAATACCTGATAGCCTTGCCCGTTTGCCGCTGGTATCTTTGAATCTCAAT GATAACAATTTAGAAGGCGAAATTCCAGAAAGTTTATCTCTTAACCCGAATCTTACTCAGTTCAAGCTCTTTAACAACAGCTTTTCA GGTATTTTGCCTCAAGATTTTGGTTTAAGTTCAGATTTGGATGAGTTTGATGTCTCTGGAAATAATCTAGAAGGTTCTTTGCCGCCC AACTTATGTTCCAGAAAGAAACTTAGGATTTTGAACCTGTTCGATAATAGGTTCAGTGGGTCAATCCCTGAATCCTATGGGGAGTGT AATTCACTAACATATGTGCGTGTTTATAATAACCAATTCTCCGGTGAAATACCAACTGGTTTCTGGAGTTTTGCTGGATACACATTT CTTGAACTGCGAAACAACAACTTTCAAGGTTCAATTCCAGCTTCAATCTCCAATGCTCGTGGTCTAACGGAAATTCTCATCTCCAGC AACAAATTCTCCGGGGAATTGCCGGCGGAAATATGCAATTTGGAAGAGATTGTGATCATGAACATAAGCAAGAATCAATTATCAGGA GAGTTGCCTTGGTGTATCACAAAGTTGAAAACATTACAAAAGTTTGATCTTTCAGAAAATAGGATCACGGGTCAAATTCCCAAATCA GTTAGTTCTTGGACCGACTTGACTGAATTGAATTTAGCTAACAATCAATTGACAGGTGAGATTCCAGGTGAGCTTGGTACTTTGCCG GTTCTGACGTACTTAGACCTCGCCGGAAACTCGCTTTCCGGCGAAATTCCATCGGAGCTGAGCAACCTCAAGCTTATCAAGTTTAAC GTATCAAATAACAGGCTTGAAGGAAAAGTGCCACTTGTGTTCGATAACGATTTTTTCTTCTCGGGTTTACAGGGCAACCCGGATCTT TGTAGTCCGGATCTTAAACCTCTGCCTGAATGTCCAAGATCCAAAAGTGTAAGCTTGTATTTGGTGTGTATTTTATCAGCTTTAGCC GTCATACTTGTCGGGTCACTTGTTTGGGTCTTGATTAAAGCCAAAAGGTTGCTACCCATCCGGAGCAAGCGTAAAAGTGCATGGAGA ATTACTGCATTTCAACGGGTTGGATTCACGGAGGGAGACTTGTTAGCTTCACTAACAAATGACAATCTCATTGGAGCTGGTGGATCG GGTCGGGTATATAGGGTCAAACTGAAAAACGGGCAGATGGTTGCGGTTAAGAAGCTTTGGGAGGCTAAACGGGAAAGAGAATCCGAG GAGGTTTTCAGGTCGGAGGTGGAGACTCTAGGGAGAGTCCGACATGGAAACATAGTAAAACTATTGTACAGTGGCATTGGTGATGAC TTCAGGATATTGGTGTATGAGTACATGGAGAATGGGAGCTTAGGAGATGTTTTACATGGGGAAAAAGGTGGCATTCTTTTGGATTGG CCAAGGAGATTTGCCATAGCAGTTGGAGCAGCTCACGGATTGGCCTATTTGCACCATGATTCTCTGCCTGCAATAGTGCACAGAGAT GTCAAGTCTAATAACATTTTGTTGGACGAGGATTTTAGGCCAAAAGTTGCTGATTTTGGTCTAGCTAAGGTAATGCAGCAGGATAGT GAGGAGAGTGATCAAGTCATGTCCCATATTGCTGGTTCCTACGGCTACATTGCACCTGAATATGCGTATACTCTGAAGATTAATGAG AAGAGTGACGTCTATAGCTTTGGTGTGTTACTTTTGGAACTAATAGCGGGTAAAAGGCCCAATGACTCCTCTTTCGGTGAGAACAAG GACATGGTCAAGTGGGTGTTAGAGGTTGCAATATCGTCTAAAAAAGATGAAGGAAGTGGCCGTGTCACGGGCAGCAATGGTATTCTT GATTTGAACCAGCTAGTCGACCAGAGAATGAATCCGTCTGCAAGCAATTATGCAGAGATTAAAAAGGTTTTTGATGTGGCTTTGCTT TGCACTTCTTCGCTGCCCATTAATAGGCCATCCATGAGAAGAGTTGTTGAATTATTGAAGGATAACAGCGTTGCTCGTTCTAAGTCA ATCCGATAG
peptide	MEHMKLQFLLLIQLFLFIIPASCLNRDIAILLRVKTGQLGDPNGLLSDWNASAPNAPCNWTGITCDRKTRKVVSIEFTSFGISGHFP ADFCRISTLKKLNVGDNSFGDSISSDSWSLCSHLHFLNLSLNFFVGKLPEFIAKFDNLTVLDVNSNNFSGDIPASLGRLPRLQELDI ANNLLNGSVPEFLSNLTELTRLVIAQNPFKPSPLPSSIGRLGKLRILYARFANLIGNIPDSIKDLKSIQNFDVAINNLTGKIPEIIG ELKTVEQIELFQNKFSGELPNTFSGLVSLFRFDASQNNLTGKIPDSLARLPLVSLNLNDNNLEGEIPESLSLNPNLTQFKLFNNSFS GILPQDFGLSSDLDEFDVSGNNLEGSLPPNLCSRKKLRILNLFDNRFSGSIPESYGECNSLTYVRVYNNQFSGEIPTGFWSFAGYTF LELRNNNFQGSIPASISNARGLTEILISSNKFSGELPAEICNLEEIVIMNISKNQLSGELPWCITKLKTLQKFDLSENRITGQIPKS VSSWTDLTELNLANNQLTGEIPGELGTLPVLTYLDLAGNSLSGEIPSELSNLKLIKFNVSNNRLEGKVPLVFDNDFFFSGLQGNPDL

	CSPDLKPLPECPRSKSVSLYLVCILSALAVILVGSLVWVLIKAKRLLPIRSKRKSAWRITAFQRVGFTEGDLLASLTNDNLIGAGGS GRVYRVKLKNGQMVAVKKLWEAKRERESEEVFRSEVETLGRVRHGNIVKLLYSGIGDDFRILVYEYMENGSLGDVLHGEKGGILLDW PRRFAIAVGAAHGLAYLHHDSLPAIVHRDVKSNNILLDEDFRPKVADFGLAKVMQQDSEESDQVMSHIAGSYGYIAPEYAYTLKINE KSDVYSFGVLLLELIAGKRPNDSSFGENKDMVKWVLEVAISSKKDEGSGRVTGSNGILDLNQLVDQRMNPSASNYAEIKKVFDVALL CTSSLPINRPSMRRVVELLKDNSVARSKSIR
Gene start	73401
Gene end	77200
Strand	-1

Nicotiana tabacum IDA-like and *HAE*-like gene families

Gene name	NtabIDA1A
SolGenomics source	N.tabacum BX Genome
SolGenomics sequence ID	gene_30902 (mRNA_52827)
SolGenomics scaffold	Ntab-BX_AWOK-SS18147
CDS	ATGGCCTCCTCCTCCTCCTCTTCCTCTTCCTCTTCCTCTTCTTCTTCTAAAAATAAAACCCTTTATTACTTAATTTGTTTGATTCTT GCCATTTCTTTTCTTGTTGGTTATGGAGTTGAAGCAAGACCAGGGAGAATGATAATGGAGGAAGAAGAAGCAAATTCAAGAATATTT TCAACACAACATTTGAAGGTATACAGAAAAGAGAATGCATACAAAACAGAAAATTTGCTATTTACTATGCTACCAAAAGGGGTTCCA ATTCCTCCTTCTGCTCCATCTAAGAGACACAATGCTTTTGTGGACTCTTCTCCTCAAAATTGA
peptide	MASSSSSSSSSSSSSSKNKTLYYLICLILAISFLVGYGVEARPGRMIMEEEEANSRIFSTQHLKVYRKENAYKTENLLFTMLPKGVP IPPSAPSKRHNAFVDSSPQN*
Gene start	707412
Gene end	707735
Strand	-1
Gene name	NtabIDA1B
SolGenomics source	N.tabacum BX Genome
SolGenomics sequence ID	gene_86896 (mRNA_146362)
SolGenomics scaffold	Ntab-BX_AWOK-SS9960
CDS	ATGGCCTCCTCCTCCTCCTCTTCCTCTTCTTCTTCTAAAAATAAAACTCTTTATTACTTAATTTGTTTGATTCTTGCCATTTCTTTT CTTCTTGGTTATGGAGTCGAAGCAAGACCAATCGAAGAAGCTAATTCAAGAATATTTTCATCACAACATTTGAAGGTATACAGAAAA GAGAATGCATACAAAACAGAAAATTTGCTATTTACTATGCTACCAAAAGGGGTTCCAATTCCTCCTTCTGCTCCATCCAAAAGGCAC AATGCTGTTATGGACTCTTCACCTCAAAATTGA
peptide	MASSSSSSSSSSKNKTLYYLICLILAISFLLGYGVEARPIEEANSRIFSSQHLKVYRKENAYKTENLLFTMLPKGVPIPPSAPSKRH NAVMDSSPQN*
Gene start	271769
Gene end	272062
Strand	1
Gene name	NtabIDA2A
SolGenomics source	N.tabacum BX Genome
SolGenomics sequence ID	–
SolGenomics scaffold	Ntab-BX_AWOK-SS12153
CDS	ATGGCTTATTCTACTAACTCTAAAACCTTTCATTTTTCATGGAATTTCATGTGCTTTATTCTTACCCTTTCTCTTGTTCTTGGCTAT GGTGCTGCAGTGAGAACAATGGCGACGGCGACGGCGAGGACGACGACGAAGAAAGAGGAAGCTTCTGGAATGTTCTCAGAGCCTGTG AAAGACTTATATGGTGAAAAGAATGAATATCTGAAAGGTAATTGGTTCAATATGCTACCAAAAGGTGTTCCTATTCCTCCTTCTGCA CCATCCAAAAGGCACAATTATTATGTGAACTCTTACCCTTAA
peptide	MAYSTNSKTFHFSWNFMCFILTLSLVLGYGAAVRTMATATARTTTKKEEASGMFSEPVKDLYGEKNEYLKGNWFNMLPKGVPIPPSA PSKRHNYYVNSYP*
Gene start	24919
Gene end	25221

Strand	-1
Gene name	NtabIDA2B
SolGenomics source	N.tabacum BX Genome
SolGenomics sequence ID	–
SolGenomics scaffold	Ntab-BX_AWOK-SS20685
CDS	ATGGCTTATTCTACTAATTCTAAAACCTTTCATTTTTCATGGAATTTCATGTGCTTGATTCTTACCCTTTCTCTTGTTCTTGGCTAT GGTGCTGCAGTGAGAACAATGGCGACAACGACGACGACGAAAGAGGAAGCTTCTGGAATGTTCTCAGAGCCTGTGAAAAACTTATAT GATGAAAAGAAAGAATTTCTGAAAGGTAATTGGTTCAATATGCTACCAAAAGGTGTTCCTATTCCTCCTTCTGCACCATCCAAAAGG CACAATTATTATGTGAACTCTTACCCTTAA
peptide	MAYSTNSKTFHFSWNFMCLILTLSLVLGYGAAVRTMATTTTTKEEASGMFSEPVKNLYDEKKEFLKGNWFNMLPKGVPIPPSAPSKR HNYYVNSYP*
Gene start	67080
Gene end	68370
Strand	-1
Gene name	NtabIDA3A
SolGenomics source	N.tabacum BX Genome
SolGenomics sequence ID	–
SolGenomics scaffold	Ntab-BX_AWOK-SS473
CDS	ATGTTGAAAAGGTTTAAAAACACAACAATATTAGTCTTACTACTTTCTCTTCATCTTCTTTTGATTTTCGTGGCTGATTATCACCAT GCAAATGCAACAAAGAACTCACAACTTTTTAATGTTAAGCCTTTGCCTAATTCCCACAATAATTCTCCGCATACATCATTTTCTCAG TCTTTGCCAAAAGGAATCCCTATTCCACCTTCTGCTCCTTCCAAAAGGCACAATGGTATCAACCTCTAA
peptide	MLKRFKNTTILVLLLSLHLLLIFVADYHHANATKNSQLFNVKPLPNSHNNSPHTSFSQSLPKGIPIPPSAPSKRHNGINL*
Gene start	166199
Gene end	166441
Strand	-1
Gene name	NtabIDA3B
SolGenomics source	N.tabacum BX Genome
SolGenomics sequence ID	–
SolGenomics scaffold	Ntab-BX_AWOK-SS2799
CDS	ATGTTGAACAGGATTAAAAACACAACAATATTAGTCTTGCTACTTTTTCTTCTTCTTCTTATCTTTATGGCTGATAATCACCATGCA AATGCAGCAAAGAACTCACAACTTTTTAATGTTAAGCCATTGACTAATTCCCACAATAATTCTCCTCACAAATCATTTTCTCAGTCT TTGCCAAAAGGAATCCCTATTCCACCTTCTGCTCCTTCCAAAAGGCACAATGGTATCAACCTCTAA
peptide	MLNRIKNTTILVLLLFLLLLIFMADNHHANAAKNSQLFNVKPLTNSHNNSPHKSFSQSLPKGIPIPPSAPSKRHNGINL*
Gene start	946688
Gene end	946927
Strand	1
Gene name	NtabIDA4A
SolGenomics source	N.tabacum BX Genome
SolGenomics sequence ID	–
SolGenomics scaffold	Ntab-BX_AWOK-SS18001
CDS	ATGGGGAAAATGAGGACAACACTATTCGTTGTTTTGCTTCTTCTTATGGTTGACCATGCTTATGCTGCAAGGGCAACGCACACACAA TTTCTCAAAGTTCAACCTTTGCATATGATGAATAAATCTCATCAATTCTCAGAGTCTTTGCCAAAAGGGGTCCCAATTCCACCTTCT GCTCCTTCCCAACGGCACAATGGTATCAACCTCAAAAGGCTAATTAGGCCATGA

peptide	MGKMRTTLFVVLLLLMVDHAYAARATHTQFLKVQPLHMMNKSHQFSESLPKGVPIPPSAPSQRHNGINLKRLIRP*
Gene start	26098
Gene end	26325
Strand	1
Gene name	NtabIDA4B
SolGenomics source	N.tabacum BX Genome
SolGenomics sequence ID	–
SolGenomics scaffold	Ntab-BX_AWOK-SS12176
CDS	ATGGGGAAAATGAGGACAATACTATTCGTTGTTTTGCTTCTTCTGATCGTTGGCCAGGTTTATGCTGCAAGGCACACACAATTTCTC AAAGTTAAGCCTTTGCATATTAATAAATCTCAATTCTCAGAGTCTTTGCCAAAAGGGGTTCCAATTCCACCTTCTGCTCCTTCCCAA AGGCACAATGGTATCAACCTCAAACAGCTTCGGCCATGA
peptide	MGKMRTILFVVLLLLIVGQVYAARHTQFLKVKPLHINKSQFSESLPKGVPIPPSAPSQRHNGINLKQLRP*
Gene start	491822
Gene end	492033
Strand	-1
Gene name	NtabIDA5A
SolGenomics source	N.tabacum BX Genome
SolGenomics sequence ID	gene_30566 (mRNA_52271)
SolGenomics scaffold	Ntab-BX_AWOK-SS18104
CDS	ATGATCAGTTTCTTCAGAAGAAAAGTACCTCTTATTCTAGTCTTTTGGATGGCTATTATATTAATCACTATTTTTGGTCATTGTCAT GGCTCAAGAAGCAGCTCTCAAGTATTTAACCCAAGTAGCCACAGAAACTCTCATCAATATGGCCATTTTTGGAATTTAATGCCAAAG AGAATTCCAATACCAGCTTCTGGTCCATCAAGAAAACACAATGATATTGGTCTTAAGAGTACTTGGAGATTACCCTAA
peptide	MISFFRRKVPLILVFWMAIILITIFGHCHGSRSSSQVFNPSSHRNSHQYGHFWNLMPKRIPIPASGPSRKHNDIGLKSTWRLP*
Gene start	315608
Gene end	315859
Strand	-1
Gene name	NtabIDA5B
SolGenomics source	N.tabacum BX Genome
SolGenomics sequence ID	gene_84812 (mRNA_142789)
SolGenomics scaffold	Ntab-BX_AWOK-SS9524
CDS	ATGATCAGTTTCTTCAGAAGAAAAGTACCTCTTATTCTAGTCTTTTGGATGGCTATTATATTAATCACTATTTTTGGTCATTGTCAT GGCTCAAGAACCAGCTCTCAAGTATTTAACCCAAGTAGCCAAAGAAACTCTCATAAATATGGCCATTTTTGGAACTTATTGCCAAAG AGAATTCCAATACCAGCTTCTGGTCCATCAAGAAAACACAATGATATTGGTCTTAAGAGTACTTGGAGATTTCCCTGA
peptide	MISFFRRKVPLILVFWMAIILITIFGHCHGSRTSSQVFNPSSQRNSHKYGHFWNLLPKRIPIPASGPSRKHNDIGLKSTWRFP*
Gene start	125323
Gene end	125574
Strand	1
Gene name	NtabHAE.1
SolGenomics source	N.tabacum BX Genome
SolGenomics sequence ID	gene_32598 (mRNA_55713)

SolGenomics scaffold	Ntab-BX_AWOK-SS18352
CDS	ATGCAACTATTCATCTTCTTTTTTAGTACTCTGCCTTTGATCTTTGCTTTAAATCAAGATGGGCTATATCTGCAAAGAATGAAGCTT TCTCTTTCCGACACAGAAGGTGCATTTTCTTCTTGGTCTGAACATGACCCTACCCCCTGTAACTGGACAGGTGTCACGTGTAACGAC GCGCCGTCTCCCTCCGTTATCGCCGTTAATCTCTCCGGCGCTTCTCTCGCCGGACCCTTCCCCATTTTCCTCTGCCACCTCCCTTTG CTTTCATCCCTCTCTCTTTCCAATAATCTTATTAACTCTACTCTTCCACTTTCTATTTCTGAATGTCGTAGCCTTACTTACCTTGAC CTTTCTCAGAATCTCGTCGGTGGCCCTATTCCTGAAACAATTGCTGATCTGCCTTACCTCAGATACCTTGATCTTAGCGGGTGCTAT TTTACGGGAGATATTCCAGCAAGTTTCGGAAAATTCCAGCAACTGGAGACTCTTATACTTACTGAAAATGTTCTTACTGGTAAAGTT CCTGCTATGTTAGGTAATGTAACGAGTCTCAGGACAATTGAACTCGCTTACAACCCATTTGCACCGAGCCAGTTTCCTCCTGAACTT GGTAACTTGACGAATCTTGAAACATTATGGCTAAGTATGTGTAATCTAGTCGGTTCAATTCCACTTAGTATTGAGAAATTGAGGCGA TTGAGTAATTTTGATGTGTCCAATAATAGACTCGTTGGGCCGATACCAAGTACAATTTTCCAGCTTAATAGTATTGTCCAAATTGAG CTCTATAACAATTCCCTTACTGGATTTTTGCCTAGTGGATGGTCTAACTTGACTAGATTGAGACGATTCGATGTGTCAACTAACAAG TTAAATGGTACTATTCCTGATGAGTTGTGTGAGTTGTCACTTGAGTCACTCAATTTATTTGAGAATCAATTTGAAGGTTTATTTCCA GAAAGTATAGCTAAGTCTCCTAATTTGTATGAGCTCAAGTTATTCTCCAACAGATTTTCAGGGTCACTGCCTAGTGAACTAGGAAAG AACTCAGCTTTACAATATCTTGATGTTTCATACAACAAATTTTCTGGTAAGATTCCAGAAAGTTTGTGTGAAATGGGAGCTTTAGAG GATCTTATTATGATTTACAATTCGTTCTCCGGGAGTATTCCAGCTAGTCTTGGTAACTGTCGGAGTTTGAGACGTGTCAGGTTTCGG GGTAATCAGCTATATGGGGAAGTCCCTACTGAGTTTTGGAGTTTGCCTCAGGTTTATCTTTTAGACCTTTTTGGCAATGCATTTTCA GGGAGTATATCACACATGATTTCTGGTGCCAAAAACTTGTCTAACTTACAAATTTCAAGAAACAGAATATCAGGGGTTATACCTTGT GAAATAGGAAAATTGCAGAATTTAGTTGAGTTTTCCGCGAGTCATAATGAGCTAACGGGAGAAATTCCAGGCACATTAGTACATCTA GGGCAGTTAGGAACCCTTGATCTTAGTTTCAATGAGTTATCAGGCGAAATCCCCTTGGGAATTCACACAATGAAGCAACTCAGTGAG CTTAACCTGGCTAGCAATAGATTTTCGGGAAAAATTCCAGATGAAATTGGGACTTTGCCAGTGCTTAATTATCTTGATCTTTCGGGG AATTACATCTCGGGTGAAATTCCACTCAGTCTGCAAAGCTTGAAGCTTAATAAGCTAAATTTGTCAAATAATCGGCTGTCCGGGACT GTTCCTGCATTTTTTGATAAGGGTGTTTATAGAAATAGCTTTCTAGGAAACCCAAGTTTGTGTCAAGGTGTTGCTGGTCTTTGTACT GCCAAAGGTGGAGGAAAGCGTGAAGGATACTTGTGGGCGTTGAGAGCTATCTACACAGTTGCTGGCTTTGTTTTTCTTGTTGGGATT GCTATGTTCATTTGGAAGTACCAGAAATTCAAGAAAATTAAGAAAGGAATCACTATATCAAAGTGGACATCATTCCATAAGCTCGGA TTCAGTGAATTTGAAATACCTTATGGCCTAGATGAAGCTAATGTAATTGGAAATGGAGCTTCAGGAAGAGTTTACAAAGCTGTCCTT AGCAATGGCGAGGCAGTAGCAGTTAAGAAGCTATGGGAGAGATCAGTTAAAGATGAAACCAGTTTTGGTGCTCTTGAGTCTGATAAA GACGAGTTTGAAATGGAAGTTGAAACTCTGGGAAAAATTAGGCACAAGAATATTGTGAGATTGTGGTGCTGTTGTGATACTGGGGAT AGCAAGCTACTGGTATATGAGTACATGCCGAATGGAAGTTTGGGCGATTTGCTGCACAGTTGCAAGGCCAAATTGTTGGATTGGCCG TTGAGGTTTAAGATAGCTTTAGATGCAGCTGAGGGGCTCTCTTATTTGCACCATGATTGTGTTCCTCCAATTGTTCACCGAGATGTT AAGTCAAACAACATATTACTGGATGGTGAATTTGGAGCAAAAATATCAGATTTTGGTGTGGCAAAAATTGTTAAAGCAGCCAGCAAA GGTGGTGCCGAATCCATGTCTGTAATTGCTGGTTCCTGTGGTTACATTGCACCAGAGTATGCATATACTCTTCATGTGAATGAAAAG AGTGACATTTATAGTTTTGGAGTGGTCATTTTGGAGCTTGTGACAGGACGAAGACCAGTTGGTCCAGAATTTGGAGAGAAAGATCTA GCTACTTGGGTACACACCACCTTGAACGAGAAAGGAGTTGATCAGTTGCTCGACCCAAATATAAATTCCAGCTTCAAAGGACATATA TGCAAAGTTCTTGATATTGGTCTATGTTGTCTTAACCATATTCCAGCTAATCGCCCCTCAATGCGCAGCGTGGTGAAAATGCTCCAA GAATCAGTTCCTTATAATGTGCCAGGGATGGTAGACAAGAATGGTAAATTTTCCCTTAGCTTTTTTCCAAAGTCAGTCCAGTGA
peptide	MQLFIFFFSTLPLIFALNQDGLYLQRMKLSLSDTEGAFSSWSEHDPTPCNWTGVTCNDAPSPSVIAVNLSGASLAGPFPIFLCHLPL LSSLSLSNNLINSTLPLSISECRSLTYLDLSQNLVGGPIPETIADLPYLRYLDLSGCYFTGDIPASFGKFQQLETLILTENVLTGKV PAMLGNVTSLRTIELAYNPFAPSQFPPELGNLTNLETLWLSMCNLVGSIPLSIEKLRRLSNFDVSNNRLVGPIPSTIFQLNSIVQIE LYNNSLTGFLPSGWSNLTRLRRFDVSTNKLNGTIPDELCELSLESLNLFENQFEGLFPESIAKSPNLYELKLFSNRFSGSLPSELGK NSALQYLDVSYNKFSGKIPESLCEMGALEDLIMIYNSFSGSIPASLGNCRSLRRVRFRGNQLYGEVPTEFWSLPQVYLLDLFGNAFS GSISHMISGAKNLSNLQISRNRISGVIPCEIGKLQNLVEFSASHNELTGEIPGTLVHLGQLGTLDLSFNELSGEIPLGIHTMKQLSE LNLASNRFSGKIPDEIGTLPVLNYLDLSGNYISGEIPLSLQSLKLNKLNLSNNRLSGTVPAFFDKGVYRNSFLGNPSLCQGVAGLCT AKGGGKREGYLWALRAIYTVAGFVFLVGIAMFIWKYQKFKKIKKGITISKWTSFHKLGFSEFEIPYGLDEANVIGNGASGRVYKAVL SNGEAVAVKKLWERSVKDETSFGALESDKDEFEMEVETLGKIRHKNIVRLWCCCDTGDSKLLVYEYMPNGSLGDLLHSCKAKLLDWP LRFKIALDAAEGLSYLHHDCVPPIVHRDVKSNNILLDGEFGAKISDFGVAKIVKAASKGGAESMSVIAGSCGYIAPEYAYTLHVNEK SDIYSFGVVILELVTGRRPVGPEFGEKDLATWVHTTLNEKGVDQLLDPNINSSFKGHICKVLDIGLCCLNHIPANRPSMRSVVKMLQ ESVPYNVPGMVDKNGKFSLSFFPKSVQ
Gene start	54701
Gene end	58000
Strand	1
Gene name	NtabHAE.2
SolGenomics source	N.tabacum BX Genome
SolGenomics sequence ID	gene_49221 (mRNA_83562)
SolGenomics scaffold	Ntab-BX_AWOK-SS2766
CDS	ATGTTAGGTAATGTAACGAGTCTCAGGACAATTGAACTCGCTTACAACCCATTTGCACCGAGCCAGTTTCCTCCTGAACTTGGTAAC TTGACGAATCTTGAGACATTATGGCTAAGTATGTGTAATCTTGTTGGTTCAATTCCACTTAATATTGAGAAATTGAGTCGATTGACT AATTTTGATGTGTCCAATAATAGACTCGTTGGGTCAATACCAAGTACAATTTTCCAGCTTAATAGTATTGTCCAAATTGAGCTATAC AATAATTCCCTTACTGGATTTTTGCCTAGTGGATGGTCTAACTTGACTAGATTGAGACGATTCGATGTGTCAACTAACAAGTTAAAT GGAACAATTCCTGATGAGTTGTGTGAGTTGTCACTTGAGTCACTCAATTTATTTGAGAATCAATTTGAAGGTTTATTTCCAGAAAGT ATAGCTAAGTCTGCTAATTTGTATGAGCTCAAGTTATTCTCTAACAGATTTTCAGGGTCATTGCCTAGTGAACTAGGAAAGAACTCT GCTTTACAGTATCTTGATGTTTCGTACAACAAATTTTCTGGTAAGATTCCAGAAAGTTTGTGTGAAATGGGAGCTTTAGAGGATCTT ATTATGATTTACAATTCGTTCTCCGGGAGTATTCCAGCTAGTCTTGGTAACTGTCGGAGTTTGAGACGTGTCAGGTTTAGGGGTAAT CAGCTATATGGGGAAGTCCCTACTGAGTTTTGGAGTTTGCCTCAGGTTTATCTTTTAGACCTTTTTGGCAATGCATTTTCAGGAAAT ATATCACACATGATTTCTGGTGCCAAAAATATGTCTAACCTGCAAATATCAAGAAACAAACTCTCAGGGGTTATACCTAGTGAAGTA

	GGAAAATTGAAGAATTTAGTTGAGTTTTCCGCGAGTCATAATGAGCTAACGGGAGAAATTCCAGGCACATTAGTGCATCTAGGTCAG TTAGGAACCCTTGATCTTAGTTTCAATGAGTTATCAGGGGAAATCCCCTTGGGAATTCACACAATGAAGCAACTCAGTGAGCTTAAC TTGGCTAACAATGGGTTTTCGGGGAAAATTCCAGATGAAATTGGGACTTTGCCAGTGCTTAATTATCTTGATCTTTCTGGGAATTAC TTCTCGGGTGAAATCCCACTCAGTCTGCAAAGCTTGAAGCTTAATAAGCTAAATTTGTCTAATAATCGTCTGTCGGGGACTGTTCCT GCATTTTTCGATAAGGGTGTTTACAGCAATAGCTTTCTAGGAAACCCAAGTTTGTGTCAAGGTGTTGCTGGTCTTTGTACTGCTAAA AGTGGAGGAAATCGTGAACGATATTTGTGGGTGTTGAGAGCTATCTATACAATTGCTGGCTTTGTTTTTCTTGTTGGGATTGCTATG TTCATTTGGAGGTACCAGAAATTCAAGAAAATTAAGAAAGGAATCACTATATCAAAGTGGACATCATTCCATAAACTCGGATTCAGT GAACTCGAAATACCTGATGGACTAGATGAAGCTAATGTAATTGGAAATGGAGCTTCGGGAAGAGTTTACAAAGCTGTCTTAAGCAAT GGTGAGGCAGTAGCAGTTAAGAAGCTATGGGAAAGATCAGTTAAAGATGAAACCGGTTTTGGTGCACTTGAGTCTGATAAAGATGAG TTTGAAATGGAAGTTGAAACTCTGGGTAAAATTAGGCACAAGAATATTGTTAGATTGTGGTGCTGTTGTGATACTGGGGATAGCAAG CTCTTGGTATATGAGTACATGCCGAATGGAAGTTTGGGCGATTTGCTGCACAGTTGCAAGGCCAAATTGTTGGATTGGCCGTTGAGA TTCAAGATAGCTTTAGATGCAGCTGAGGGACTCTCTTATTTGCACCATGATTGTGTTCCTCCAATTGTTCACCGAGATGTTAAGTCA AACAACATATTACTGGATGGTGAGTTTGGCGCCAAAATTTCAGATTTTGGTGTGGCGAAAATTGTTAAAGCAGCCAGCAAAGGTGGT GCCGAATCCATGTCCGTAATTGCTGGTTCCTGTGGTTACATTGCACCAGAGTATGCATATACTCTTCATGTGAATGAAAAGAGCGAT ATTTATAGCTTTGGAGTGGTCATCTTGGAGCTGGTGACAGGCAGAAGACCAGTTGGTCCAGAATTTGGGGAGAAAGATCTAGCTACT TGGGTACGCACCACCTTGAACGAGAAAGGAGTTGATCAGTTGCTCGACCCAAATTTAAATTCCACCTTCAAAGAACATATATGCAAA GTTCTTGATATTGGTCTATGTTGTCTTAACCATATTCCAGCTAATCGCCCCTCAATGCGCAGAGTTGTGAAAATGCTCCAAGAATCA TTTCCTTATAATGTGCCAGGGATGGTAAACAAGAATGGTAAACTTCTCCCTTACTTTTTTCCAAAGTCAGTCTAG
peptide	MLGNVTSLRTIELAYNPFAPSQFPPELGNLTNLETLWLSMCNLVGSIPLNIEKLSRLTNFDVSNNRLVGSIPSTIFQLNSIVQIELY NNSLTGFLPSGWSNLTRLRRFDVSTNKLNGTIPDELCELSLESLNLFENQFEGLFPESIAKSANLYELKLFSNRFSGSLPSELGKNS ALQYLDVSYNKFSGKIPESLCEMGALEDLIMIYNSFSGSIPASLGNCRSLRRVRFRGNQLYGEVPTEFWSLPQVYLLDLFGNAFSGN ISHMISGAKNMSNLQISRNKLSGVIPSEVGKLKNLVEFSASHNELTGEIPGTLVHLGQLGTLDLSFNELSGEIPLGIHTMKQLSELN LANNGFSGKIPDEIGTLPVLNYLDLSGNYFSGEIPLSLQSLKLNKLNLSNNRLSGTVPAFFDKGVYSNSFLGNPSLCQGVAGLCTAK SGGNRERYLWVLRAIYTIAGFVFLVGIAMFIWRYQKFKKIKKGITISKWTSFHKLGFSELEIPDGLDEANVIGNGASGRVYKAVLSN GEAVAVKKLWERSVKDETGFGALESDKDEFEMEVETLGKIRHKNIVRLWCCCDTGDSKLLVYEYMPNGSLGDLLHSCKAKLLDWPLR FKIALDAAEGLSYLHHDCVPPIVHRDVKSNNILLDGEFGAKISDFGVAKIVKAASKGGAESMSVIAGSCGYIAPEYAYTLHVNEKSD IYSFGVVILELVTGRRPVGPEFGEKDLATWVRTTLNEKGVDQLLDPNLNSTFKEHICKVLDIGLCCLNHIPANRPSMRRVVKMLQES FPYNVPGMVNKNGKLLPYFFPKSV
Gene start	217401
Gene end	220500
Strand	-1
Gene name	NtabHSL1.1
SolGenomics source	N.tabacum BX Genome
SolGenomics sequence ID	gene_63539 (mRNA_106017)
SolGenomics scaffold	Ntab-BX_AWOK-SS4971
CDS	ATGTTTCTTCAAATCTTTGTTACTCTTTTGTTCCCAACTTTGATTTTCTCACTTAACCAAGAGGGTCTGTATTTACACAACGTGAAG CTCGGATTTGATGACCCTGATAGTGTTCTTTCCAACTGGAATGAGCACGACGAGACACCGTGTAACTGGTTTGGCATAACCTGTGAT CAAACAACTCGGTCCGTTACATCCTTGGACCTCGCCAATGCTAACGTTGCTGGTCCTTTTCCTTCACTTCTCTGTCGGTTGAAGAAA CTGCGTTACATTTCGTTATACAACAACGCTGTTAACTCCACCCTTCCTGAAGATTTTTCCGGGTGTGAATCTTTGGAGCATCTCGAT TTGGCTCAGAACTTTTTGGTCGGTACACTTCCGGCGAGTTTACCTGAGCTTCCGAATTTGAAATACCTTGACTTGGGGGGAAACAAC TTTACCGGCGACATTCCGTCAAGTTTCGGTTCTTTCCGGCAGCTGGAGGTTCTTGGACTGGTTGGGAACTTGCTGGACGGGACTATT CCAGCGTTTCTGGGTAACATTTCGACGTTAAAGCAGCTGAATCTGTCGTACAACCCGTTTTCGACGGGTCAGATCCCGCCGGAGCTG GGAAATCTGACAAATCTCGAGGTTTTGTGGCTCTCGGACTGTAATTTGGTCGGTGAAGTTCCTGATACATTGGGTCGGTTGAAGAAG ATTGTGGATTTGGACCTTGCTGTGAACTACTTGGATGGGCCGATCCCGAGTTGGCTCACTGAGTTAACTAGTGCTGAACAAATTGAG CTGTATAACAACTCGTTCACCGGCGAGTTACCGGCGAATGGGTGGTCGAAAATGACGGCGTTAAGGCGACTCGACGTGTCGATGAAT CGGGTCACGGGTACGGTTCCGAGGGAGTTGTGTGAGTTGCCACTTGAGTCGCTGAATCTGTATGAGAACCAAATGTTTGGTGAATTG CCACAAGGCATTGCGAACTCGCCGAATTTGTACGAGTTGCGGCTTTTTCACAACCGTTTTAATGGTAGTTTGCCTAAAGATCTTGGG AAGAATTCACCTTTGTTGTGGATTGATGTGTCTGAGAATAAATTTTCTGGTGAAATTCCGGAGAATTTGTGTGGGAAAGGGTTTTTG GAAGAGCTTTTGATGATAGATAACGTACTTACTGGTGAAATTCCGGCGAGTTTGAGTGAATGCAGGAGCTTATTGCGGGTGAGATTG GCTCACAATCAATTATCTGGTGATGTTCCGGCGGGTTTCTGGGGCCTACCACACCTTTCCCTGCTTGAGCTCGTGGACAATTCACTA TCTGGTGATATCGCAAAAACTATAGCTAGTGCTTCAAATTTATCAGCTTTGATTTTGTCCAAGAACAAATTTTCAGGTCCCATTCCA GAGGAGATTGGTTCTCTGGAAAATATTCTTGATTTTGTGGGCAACGATAACCAGTTTTCTGGGGCTTTGCCAGCTAGTTTAGTGATG CTGGGACAATTGGGAAGGCTGGATCTTCACAACAATGAGTTAAATGGTGAGCTTCCAAGTGGGATTCATTCTTTGAAGAGGTTGAAT GAATTGAACTTGGCAAACAATTATCTTTCGGGAGCTATCCCCAAGGAAATTGGGGGCTTGTCTGTTTTGAATTATCTTGATCTATCA GGGAACCAGTTTACAGGGAAGATCCCAATGGAGTTGCAGAATTTGAAGCTTAATCAGCTGAACTTGTCGAACAATGACCTTTCGGGT GATATTCCCCCTTTGTATGCAAAGGAAATGTATAGGAGTAGCTTTTTGGGGAATGCTGGTTTATGTGGAGACATCGAGGGCTTGTGT GAAGGAACAGCTGAAGGTAAAACTGCTGGTTATGTTTGGTTATTGAGGTTACTCTTTACTCTTGCTGGATTGGTGTTTGTAGTTGGG GTGGTTTGGTTCTATTGGAAGTATAAGAATTTTAAGAAAGCTAAAATGGCTATTGATAAGTCTAAATGGACTTTGATGTCGTTTCAT AAGTTGGGTTTCAATGAGTATGAAATCTTGGATGCTCTTGATGAGGACAACTTAATTGGAAGTGGCGCTTCCGGGAAGGTTTACAAG GTTGTTCTGAGCAAGGGTGACACTGTTGCGGTGAAGAAGATTTTGAGAAACACGAAAATAACAGATGAGAGTAGTGATATCGAGAAG GGTAGCATTCAAGATGATGGATTTGAAGCGGAGGTTGAGACATTGGGGAAGATACGGCACAAGAACATTGTTAAGCTATGGTGTTGT TGTACAACAAGGGATTGCAAACTTCTGGTTTACGAGTACATGCCTAATGGAAGCTTGGGTGATTTGCTACACAGCAGCAAAAGCGGC CTTCTAGACTGGCCTATGAGATATAAGATAGCCATGGATGCTGCTGAGGGACTCTCTTACTTGCATCATGACTGTGCTCCGCCGATT GTTCACAGAGATGTTAAGTCAAACAACATCTTGTTGGATGGTGATTTTGGAGCTCGAGTTGCTGATTTTGGTGTAGCGAAGGCGGTC GATGCCAATGCCAAGGGAATCAAGTCCATGTCTGTCATTGCAGGGTCTTGTGGTTACATTGCTCCAGAATATGCATATACACTGCGG

	GTGAACGAGAAGAGCGATATATACAGCTTCGGTGTGGTAATCCTAGAGCTTGTGACTGGGAAGCGCCCTGTGGATCCCGAATTCGGG GAAAAGGATTTGGTGAAGTGGGTATGCTCTACACTGGACCAGAAGGGTGTAGATCATGTAATTGACCCTAAACATGATTCTTGTTTC AAGGAGGAGATATGCAAGGTCTTAAATATTGGCCTCCTCTGCACTAGCCCTCTCCCAATCAACCGACCCTCGATGAGACGGGTCGTA AAAATGTTGCAAGAAGTGGGTGCTGGGAACCTGCCCAAGGCTGCTTCTAAGGATGGCAAATTGACTCCTTATTACTATGAAGAAGCA TCAGATCAAGGAAGTGTAGCTTAA
peptide	MFLQIFVTLLFPTLIFSLNQEGLYLHNVKLGFDDPDSVLSNWNEHDETPCNWFGITCDQTTRSVTSLDLANANVAGPFPSLLCRLKK LRYISLYNNAVNSTLPEDFSGCESLEHLDLAQNFLVGTLPASLPELPNLKYLDLGGNNFTGDIPSSFGSFRQLEVLGLVGNLLDGTI PAFLGNISTLKQLNLSYNPFSTGQIPPELGNLTNLEVLWLSDCNLVGEVPDTLGRLKKIVDLDLAVNYLDGPIPSWLTELTSAEQIE LYNNSFTGELPANGWSKMTALRRLDVSMNRVTGTVPRELCELPLESLNLYENQMFGELPQGIANSPNLYELRLFHNRFNGSLPKDLG KNSPLLWIDVSENKFSGEIPENLCGKGFLEELLMIDNVLTGEIPASLSECRSLLRVRLAHNQLSGDVPAGFWGLPHLSLLELVDNSL SGDIAKTIASASNLSALILSKNKFSGPIPEEIGSLENILDFVGNDNQFSGALPASLVMLGQLGRLDLHNNELNGELPSGIHSLKRLN ELNLANNYLSGAIPKEIGGLSVLNYLDLSGNQFTGKIPMELQNLKLNQLNLSNNDLSGDIPPLYAKEMYRSSFLGNAGLCGDIEGLC EGTAEGKTAGYVWLLRLLFTLAGLVFVVGVVWFYWKYKNFKKAKMAIDKSKWTLMSFHKLGFNEYEILDALDEDNLIGSGASGKVYK VVLSKGDTVAVKKILRNTKITDESSDIEKGSIQDDGFEAEVETLGKIRHKNIVKLWCCCTTRDCKLLVYEYMPNGSLGDLLHSSKSG LLDWPMRYKIAMDAAEGLSYLHHDCAPPIVHRDVKSNNILLDGDFGARVADFGVAKAVDANAKGIKSMSVIAGSCGYIAPEYAYTLR VNEKSDIYSFGVVILELVTGKRPVDPEFGEKDLVKWVCSTLDQKGVDHVIDPKHDSCFKEEICKVLNIGLLCTSPLPINRPSMRRVV KMLQEVGAGNLPKAASKDGKLTPYYYEEASDQGSVA
Gene start	8301
Gene end	12000
Strand	1
Gene name	NtabHSL1.2
SolGenomics source	N.tabacum BX Genome
SolGenomics sequence ID	gene_63539 (mRNA_106018)
SolGenomics scaffold	Ntab-BX_AWOK-SS11846
CDS	ATGTTTCTTCAAATCTTTGTTACTCTTTTGTTCCCAACTTTGATTTTCTCACTTAACCAAGAGGGTCTGTATTTACACAACGTGAAG CTCGGATTTGATGACCCTGATAGTGTTCTTTCCAACTGGAATGAGCACGACGAGACACCGTGTAACTGGTTTGGCATAACCTGTGAT CAAACAACTCGGTCCGTTACATCCTTGGACCTCGCCAATGCTAACGTTGCTGGTCCTTTTCCTTCACTTCTCTGTCGGTTGAAGAAA CTGCGTTACATTTCGTTATACAACAACGCTGTTAACTCCACCCTTCCTGAAGATTTTTCCGGGTGTGAATCTTTGGAGCATCTCGAT TTGGCTCAGAACTTTTTGGTCGGTACACTTCCGGCGAGTTTACCTGAGCTTCCGAATTTGAAATACCTTGACTTGGGGGGAAACAAC TTTACCGGCGACATTCCGTCAAGTTTCGGTTCTTTCCGGCAGCTGGAGGTTCTTGGACTGGTTGGGAACTTGCTGGACGGGACTATT CCAGCGTTTCTGGGTAACATTTCGACGTTAAAGCAGCTGAATCTGTCGTACAACCCGTTTTCGACGGGTCAGATCCCGCCGGAGCTG GGAAATCTGACAAATCTCGAGGTTTTGTGGCTCTCGGACTGTAATTTGGTCGGTGAAGTTCCTGATACATTGGGTCGGTTGAAGAAG ATTGTGGATTTGGACCTTGCTGTGAACTACTTGGATGGGCCGATCCCGAGTTGGCTCACTGAGTTAACTAGTGCTGAACAAATTGAG CTGTATAACAACTCGTTCACCGGCGAGTTACCGGCGAATGGGTGGTCGAAAATGACGGCGTTAAGGCGACTCGACGTGTCGATGAAT CGGGTCACGGGTACGGTTCCGAGGGAGTTGTGTGAGTTGCCACTTGAGTCGCTGAATCTGTATGAGAACCAAATGTTTGGTGAATTG CCACAAGGCATTGCGAACTCGCCGAATTTGTACGAGTTGCGGCTTTTTCACAACCGTTTTAATGGTAGTTTGCCTAAAGATCTTGGG AAGAATTCACCTTTGTTGTGGATTGATGTGTCTGAGAATAAATTTTCTGGTGAAATTCCGGAGAATTTGTGTGGGAAAGGGTTTTTG GAAGAGCTTTTGATGATAGATAACGTACTTACTGGTGAAATTCCGGCGAGTTTGAGTGAATGCAGGAGCTTATTGCGGGTGAGATTG GCTCACAATCAATTATCTGGTGATGTTCCGGCGGGTTTCTGGGGCCTACCACACCTTTCCCTGCTTGAGCTCGTGGACAATTCACTA TCTGGTGATATCGCAAAAACTATAGCTAGTGCTTCAAATTTATCAGCTTTGATTTTGTCCAAGAACAAATTTTCAGGTCCCATTCCA GAGGAGATTGGTTCTCTGGAAAATATTCTTGATTTTGTGGGCAACGATAACCAGTTTTCTGGGGCTTTGCCAGCTAGTTTAGTGATG CTGGGACAATTGGGAAGGCTGGATCTTCACAACAATGAGTTAAATGGTGAGCTTCCAAGTGGGATTCATTCTTTGAAGAGGTTGAAT GAATTGAACTTGGCAAACAATTATCTTTCGGGAGCTATCCCCAAGGAAATTGGGGGCTTGTCTGTTTTGAATTATCTTGATCTATCA GGGAACCAGTTTACAGGGAAGATCCCAATGGAGTTGCAGAATTTGAAGCTTAATCAGCTGAACTTGTCGAACAATGACCTTTCGGGT GATATTCCCCCTTTGTATGCAAAGGAAATGTATAGGAGTAGCTTTTTGGGGAATGCTGGTTTATGTGGAGACATCGAGGGCTTGTGT GAAGGAACAGCTGAAGGTAAAACTGCTGGTTATGTTTGGTTATTGAGGTTACTCTTTACTCTTGCTGGATTGGTGTTTGTAGTTGGG GTGGTTTGGTTCTATTGGAAGTATAAGAATTTTAAGAAAGCTAAAATGGCTATTGATAAGTCTAAATGGACTTTGATGTCGTTTCAT AAGTTGGGTTTCAATGAGTATGAAATCTTGGATGCTCTTGATGAGGACAACTTAATTGGAAGTGGCGCTTCCGGGAAGGTTTACAAG GTTGTTCTGAGCAAGGGTGACACTGTTGCGGTGAAGAAGATTTTGAGAAACACGAAAATAACAGATGAGAGTAGTGATATCGAGAAG GGTAGCATTCAAGATGATGGATTTGAAGCGGAGGTTGAGACATTGGGGAAGATACGGCACAAGAACATTGTTAAGCTATGGTGTTGT TGTACAACAAGGGATTGCAAACTTCTGGTTTACGAGTACATGCCTAATGGAAGCTTGGGTGATTTGCTACACAGCAGCAAAAGCGGC CTTCTAGACTGGCCTATGAGATATAAGATAGCCATGGATGCTGCTGAGGGACTCTCTTACTTGCATCATGACTGTGCTCCGCCGATT GTTCACAGAGATGTTAAGTCAAACAACATCTTGTTGGATGGTGATTTTGGAGCTCGAGTTGCTGATTTTGGTGTAGCGAAGGCGGTC GATGCCAATGCCAAGGGAATCAAGTCCATGTCTGTCATTGCAGGGTCTTGTGGTTACATTGCTCCAGAATATGCATATACACTGCGG GTGAACGAGAAGAGCGATATATACAGCTTCGGTGTGGTAATCCTAGAGCTTGTGACTGGGAAGCGCCCTGTGGATCCCGAATTCGGG GAAAAGGATTTGGTGAAGTGGGTATGCTCTACACTGGACCAGAAGGGTGTAGATCATGTAATTGACCCTAAACATGATTCTTGTTTC AAGGAGGAGATATGCAAGGTCTTAAATATTGGCCTCCTCTGCACTAGCCCTCTCCCAATCAACCGACCCTCGATGAGACGGGTCGTA AAAATGTTGCAAGAAGTGGGTGCTGGGAACCTGCCCAAGGCTGCTTCTAAGGATGGCAAATTGACTCCTTATTACTATGAAGAAGCA TCAGATCAAGGAAGTGTAGCTTAA
peptide	MFLQIFVTLLFPTLIFSLNQEGLYLHNVKLGFDDPDNVLSNWNEHDETPCNWFGITCDKTTRSVTSLDLANANVAGPFPSLLCRLKK LRYISLYNNAVNSTLPEDFSGCESLEHLDLAQNFLVGTLPASLPALPNLKYLDLSGNNFTGDIPASFGSFRQLEVLGLVGNLLDGTI PAFLGNISTLKQLNLSYNPFSTGRIPPELGNLTNLEVLWLSDCNLVGEVPDTLGRLKNIVDLDLAVNYLDGPIPSWLTELTNAEQIE LYNNSFTGELPVNGWSKMTALRRLDVSMNRVTGTVPRELCELPLESLNLYENQMFGELPQGIANSPNLYELRLFHNRFNGSLPKDLG KNSPLLWIDVSENKFSGELPENLCGKGFLEELLMIDNLLTGEIPASLSECRSLLRVRLAHNQFSGDVPAGFWGLPHLSLLELMDNSL SGDIAKTIASASNLSALILSKNKFSGPIPEEIGSLENLLDFVGNDNLFSGPLPASLVMLGQLGRLDLHNNELIGELPSGIHSLKKLN

	ELNLANNDLSGAIPKEIGSLSVLNYLDLSGNQFSGKIPMELQNLKLNQLNLSNNDLSGDIPPLYAKEMYKSSLFGNAGLCGDIEGLC EGTAEGKTAGYVWLLRLLFTLAGLVFVVGVVWFYWKYKNFKKANMAIDKSKWTLMSFHKLGFNEYEILDALDEDNLIGSGASGKVYK VVLSKGDTVAVKKILRSAKITDDSSDIEKGSIQDDGFEAEVETLGKIRHKNIVKLWCCCTTRDCKLLVYEYMPNGSLGDLLHSSKSG LLDWPMRYKIAMDAAEGLSYLHHDCAPPIVHRDVKSNNILLDGDFGARVADFGVAKAVDANAKGIKSMSVIAGSCGYIAPEYAYTLR VNEKSDIYSFGVVILELVTGKRPVDPEFGEKDLVKWVCSTLDQKGVDHVIDPKHDSCFKEEICKVLNIGLLCTSPLPINRPSMRRVV KMLQEVGAGNLPKAASKDGKLTPYYYEEASDQGSVA
Gene start	218301
Gene end	222000
Strand	1
Gene name	NtabHSL2.1
SolGenomics source	N.tabacum BX Genome
SolGenomics sequence ID	gene_66081 (mRNA_110390)
SolGenomics scaffold	Ntab-BX_AWOK-SS5522
CDS	ATGGAACACACGAAACTCCAATTTCTGCTACTCATACAACTGTTTCTATTCATTATTCCGGCTAGTTGCTTGAACCGCGATATCGCC ATTTTACTCCGGGTTAAGACAGGTCAGCTCGGTGACCCCAATGGATTGCTCTCTGATTGGAACGCGTCTGCTCCAAATGCGCCTTGT AACTGGACCGGCATTACCTGTGATCGTAAAACGCATAAGGTTGTCTCCATCGAGTTCACCAGTTTTGGAATCTCAGGTCATTTTCCG GCCGACTTCTGCCGGATTTCGACTTTGCAGAAACTCAATCTGGGCGATAACAGTTTCGGTGACTCTATTTCCTCTGACTCCTGGTCC CTATGTTCGCATCTGCACTTTTTGAATCTTTCTTTAAATTTCTTCGTTGGCAAGCTGCCGGAGTTTATAGCCAAGTTTGATAACTTG ACCGTGCTTGATGTTAATTCAAACAATTTCTCCGGTGATATTCCGGCGAGCTTAGGCCGGTTACCGAGATTACAAGAGCTCGATATT GCCAACAATCTCCTTAATGGTTCAGTTCCTGAGTTCTTATCCAATCTCACCGAGTTGACTCGATTGGTCATTGCTCAAAATCCATTT AAGCCAAGTCCATTGCCTTCCTCAATTGGACGACTAGGTAAACTTCGAATTCTATATGCTCGGTTTGCGAATCTTATTGGAAATATT CCAGATTCCATTAAAGACCTGAAATCTATTCAGAATTTTGACGTGGCGATTAACAATCTAACTGGAAAAATTCCAGAAAGCATTGGA GAGCTGAAAACCGTAGAACAAATAGAGCTCTTTCAGAATAAATTTTCAGGTGAACTGCCGAACACGTTTTCGGGACTTGTTTCTCTG TTCAGGTTTGACGCTTCTCAGAATAATCTCACCGGAAAAATACCTGATAGCCTTGCCCGTTTGCCGCTGGTATCTTTGAATCTCAAT GATAACAATTTAGAAGGCGAAATTCCAGAAAGTTTAGCTCTTAACCCGAATCTTACTCAGTTCAAGCTCTTTAACAACAAATTTTCA GGTACTTTACCTCAAGATTTTGGTATGAGTTCAGATTTGGATGAGTTTGATGTCTCTGGCAATAATCTCGAAGGTTCTTTGCCCCCC AATTTATGTTCCAGAAAGAAACTTAGGATTTTGAACCTGTTCGATAATAGGTTCAGTGGTTCAGTCCCTGAATCCTATGGGGAGTGT AATTCACTAACGTACGTGCGTATCTATAACAACCAATTCTCTGGTGAATTACCAACTGGTTTCTGGAGTTTTGCTGGATACACATTT CTTGAACTGAGAAACAACAACTTTCAAGGTTCAATTCCAGCTTCAATCTCCAATGCTCGTGGCCTAACAGAAATTCTCATCTCCGGT AACAAATTCTCCGAGGAATTGCCGGCGGGATTATGCAATTTGGAAGAGATTGTGATTATGGACATAAGCAAGAATCAATTATCAGGA GATTTGCCTTCATGTATCACAAAGATGAAAACGTTACAAAAGCTTGATCTTTCAGAAAATAGGATCACGGGTCAAATTCCCAAATTA GTTAGTTCTTGGACCGACTTGACTGAACTGAATTTAGCTAACAATCAATTGACAGGTGAAATTCCAGGTGAGCTTGGGACTTTGCCG GTTTTGACGTACTTAGACCTCGCTGGAAACTCGCTTTCCGGCGAAATTCCGTCGGAGCTGAGCAACCTCAAGCTTAACAAGTTCAAC GTATCAAATAACAGGCTTGAAGGAAAAGTGCCACTTGTGTTTGATAATGATTTTTTCATCTCGGGTTTGCAGGGCAATCCGGATCTT TGTAGTCCGGATCTTAAACCTCTACCTCAGTGCCCAAGACCCAAAAGTATTAGCTTGTATTTGGTGTGTATTTTATCAGCTTTATCC GTCATACTTGTCGGGTCACTTGTTTGGGTCTTGATCAAGGCCAAAAAGTTGCTACCCATTCGGAGTAAGCGTAAAAGTGCATGGAGA ATTACTGCATTTCAACGGGTTGGATTCACGGAGGGAGACTTGTTAGCTTCACTGACAAATGAGAATCTCATTGGAGCTGGTGGGTCT GGTCGGGTATATAGGGTCAAACTAAAAAACGGGCAGATGGTCGCGGTTAAGAAGCTTTGGGAGGCTAAACGGGAGAGAGAATCTGAG GAGGTTTTCAGGTCGGAGGTGGAGACTCTAGGGAGAGTCCGACATGGAAACATAGTAAAACTATTGTACAGTGGCATTGGTGACCAC TTCAGGATATTGGTGTATGAGTACATGGAAAATGGGAGCTTAGGAGATGTATTACATGGGGAAAAAGGTGGCATTCTTTTGGATTGG CCAAGGAGATTTGGCATAGCAGTTGGAGCAGCTCAAGGATTGGCCTATTTGCACCATGATTCTGTTCCTGCAATAGTGCACAGAGAT GTCAAGTCTAATAACATTTTGTTGGACGAGGATTTTAGGCCAAAAGTTGCTGATTTTGGGCTAGCTAAGGTAATGCAGCAGGACAGT GAGGAGAGTGATCAAGTCATGTCCCATATTGCTGGTTCCTACGGCTACATTGCACCTGAATATGCGTATACTCTGAAGATTAATGAG AAGAGTGACGTTTATAGCTTTGGTGTGGTACTGTTGGAACTAATAACCGGTAAAAGGCCCAATGACTCCTCTTTCGGTGAGAACAAG GACATGGTCAAGTGGGTGTTAGAGGTTGCAATATCGTCTAAAAAAGATGAAGGAAGTGGCCGTGTCACGGGCAGCAATAGTATTCTT GATTTGAACCAGCTAGTCGACCAGAGAATGAATCCGTCTGCAAGCAATTATGCAGAGATTAAAAAGGTTTTTGATGTGGCTTTGCTT TGCACTTCTTCATTGCCCATTAACAGGCCGTCCATGAGAAGAGTTGTTGAATTGTTGAAGGATAACAGTGTTGCTCGTTCTAAGTCA ATCCGATAG
peptide	MEHTKLQFLLLIQLFLFIIPASCLNRDIAILLRVKTGQLGDPNGLLSDWNASAPNAPCNWTGITCDRKTHKVVSIEFTSFGISGHFP ADFCRISTLQKLNLGDNSFGDSISSDSWSLCSHLHFLNLSLNFFVGKLPEFIAKFDNLTVLDVNSNNFSGDIPASLGRLPRLQELDI ANNLLNGSVPEFLSNLTELTRLVIAQNPFKPSPLPSSIGRLGKLRILYARFANLIGNIPDSIKDLKSIQNFDVAINNLTGKIPESIG ELKTVEQIELFQNKFSGELPNTFSGLVSLFRFDASQNNLTGKIPDSLARLPLVSLNLNDNNLEGEIPESLALNPNLTQFKLFNNKFS GTLPQDFGMSSDLDEFDVSGNNLEGSLPPNLCSRKKLRILNLFDNRFSGSVPESYGECNSLTYVRIYNNQFSGELPTGFWSFAGYTF LELRNNNFQGSIPASISNARGLTEILISGNKFSEELPAGLCNLEEIVIMDISKNQLSGDLPSCITKMKTLQKLDLSENRITGQIPKL VSSWTDLTELNLANNQLTGEIPGELGTLPVLTYLDLAGNSLSGEIPSELSNLKLNKFNVSNNRLEGKVPLVFDNDFFISGLQGNPDL CSPDLKPLPQCPRPKSISLYLVCILSALSVILVGSLVWVLIKAKKLLPIRSKRKSAWRITAFQRVGFTEGDLLASLTNENLIGAGGS GRVYRVKLKNGQMVAVKKLWEAKRERESEEVFRSEVETLGRVRHGNIVKLLYSGIGDHFRILVYEYMENGSLGDVLHGEKGGILLDW PRRFGIAVGAAQGLAYLHHDSVPAIVHRDVKSNNILLDEDFRPKVADFGLAKVMQQDSEESDQVMSHIAGSYGYIAPEYAYTLKINE KSDVYSFGVVLLELITGKRPNDSSFGENKDMVKWVLEVAISSKKDEGSGRVTGSNSILDLNQLVDQRMNPSASNYAEIKKVFDVALL CTSSLPINRPSMRRVVELLKDNSVARSKSIR
Gene start	246701
Gene end	250400
Strand	1

Gene name	NtabHSL2.2
SolGenomics source	N.tabacum BX Genome
SolGenomics sequence ID	gene_29102 (mRNA_49768)
SolGenomics scaffold	Ntab-BX_AWOK-SS17840
CDS	ATGGAACACATGAAACTCCAATTTCTGCTACTCATCCAACTGTTTTTATTCATTATTCCGGCGAGTTGCTTGAACCGCGATATTGCC ATTTTACTCCGGGTTAAAACTGGTCAGCTCGGTGACCCCAATGGGTTGCTCTCTGATTGGAACGCATCAGCTCCAAATGCGCCTTGT AACTGGACTGGCATTACCTGTGATCGTAAAACGCGTAAGGTTGTCTCCATCGAGTTCACCAGTTTTGGAATCTCCGGTCATTTTCCG GCCGACTTTTGCCGGATTTCGACTTTGAAGAAACTCAATGTCGGCGATAACAGTTTCGGTGACTCTATTTCCTCCGACTCCTGGTCT CTATGTTCGCATCTGCACTTTTTGAATCTTTCTTTAAATTTCTTCGTTGGCAAGCTACCGGAGTTTATAGCCAAGTTTGATAACTTG ACCGTCCTTGATGTTAATTCAAACAATTTCTCCGGTGATATTCCGGCGAGCTTAGGCCGGTTACCGAGATTACAAGAGCTCGATATT GCCAACAATCTCCTTAATGGTTCAGTTCCTGAGTTCTTATCCAATCTTACCGAGTTGACTCGATTGGTCATTGCTCAAAATCCATTT AAGCCAAGTCCATTGCCTTCCTCAATCGGACGACTAGGTAAACTTCGAATTCTATATGCTCGGTTTGCGAATCTTATTGGAAATATT CCAGATTCCATTAAGGACCTGAAATCTATTCAGAATTTTGACGTGGCAATCAACAATCTTACTGGAAAAATTCCAGAAATCATTGGA GAACTGAAAACCGTAGAACAAATAGAGCTTTTTCAGAATAAATTTTCAGGTGAATTGCCGAACACGTTTTCGGGACTTGTTTCTCTG TTCAGGTTTGACGCTTCTCAGAACAATCTCACGGGAAAAATACCTGATAGCCTTGCCCGTTTGCCGCTGGTATCTTTGAATCTCAAT GATAACAATTTAGAAGGCGAAATTCCAGAAAGTTTATCTCTTAACCCGAATCTTACTCAGTTCAAGCTCTTTAACAACAGCTTTTCA GGTATTTTGCCTCAAGATTTTGGTTTAAGTTCAGATTTGGATGAGTTTGATGTCTCTGGAAATAATCTAGAAGGTTCTTTGCCGCCC AACTTATGTTCCAGAAAGAAACTTAGGATTTTGAACCTGTTCGATAATAGGTTCAGTGGGTCAATCCCTGAATCCTATGGGGAGTGT AATTCACTAACATATGTGCGTGTTTATAATAACCAATTCTCCGGTGAAATACCAACTGGTTTCTGGAGTTTTGCTGGATACACATTT CTTGAACTGCGAAACAACAACTTTCAAGGTTCAATTCCAGCTTCAATCTCCAATGCTCGTGGTCTAACGGAAATTCTCATCTCCAGC AACAAATTCTCCGGGGAATTGCCGGCGGAAATATGCAATTTGGAAGAGATTGTGATCATGAACATAAGCAAGAATCAATTATCAGGA GAGTTGCCTTGGTGTATCACAAAGTTGAAAACATTACAAAAGTTTGATCTTTCAGAAAATAGGATCACGGGTCAAATTCCCAAATCA GTTAGTTCTTGGACCGACTTGACTGAATTGAATTTAGCTAACAATCAATTGACAGGTGAGATTCCAGGTGAGCTTGGTACTTTGCCG GTTCTGACGTACTTAGACCTCGCCGGAAACTCGCTTTCCGGCGAAATTCCATCGGAGCTGAGCAACCTCAAGCTTATCAAGTTTAAC GTATCAAATAACAGGCTTGAAGGAAAAGTGCCACTTGTGTTCGATAACGATTTTTTCGTCTCGGGTTTACAGGGCAACCCGGATCTT TGTAGTCCGGATCTTAAACCTCTGCCTGAATGTCCAAGATCCAAAAGTGTAAGCTTGTATTTGGTGTGTATTTTATCAGCTTTAGCC GTCATACTTGTCGGGTCACTTGTTTGGGTCTTGATTAAAGCCAAAAGGTTGCTACCCATCCGGAGCAAGCGTAAAAGTGCATGGAGA ATTACTGCATTTCAACGGGTTGGATTCACGGAGGGAGACTTGTTAGCTTCACTAACAAATGACAATCTCATTGGAGCTGGTGGATCG GGTCGGGTATATAGGGTCAAACTGAAAAACGGGCAGATGGTTGCGGTTAAGAAGCTTTGGGAGGCTAAACGGGAAAGAGAATCCGAG GAGGTTTTCAGGTCGGAGGTGGAGACTCTAGGGAGAGTCCGACATGGAAACATAGTAAAACTATTGTACAGTGGCATTGGTGATGAC TTCAGGATATTGGTGTATGAGTACATGGAGAATGGGAGCTTAGGAGATGTTTTACATGGGGAAAAAGGTGGCATTCTTTTGGATTGG CCAAGGAGATTTGCCATAGCAGTTGGAGCAGCTCACGGATTGGCCTATTTGCACCATGATTCTCTGCCTGCAATAGTGCACAGAGAT GTCAAGTCTAATAACATTTTGTTGGACGAGGATTTTAGGCCAAAAGTTGCTGATTTTGGTCTAGCTAAGGTAATGCAGCAGGATAGT GAGGAGAGTGATCAAGTCATGTCCCATATTGCTGGTTCCTACGGCTACATTGCACCTGAATATGCGTATACTCTGAAGATTAATGAG AAGAGTGACGTCTATAGCTTTGGTGTGTTACTTTTGGAACTAATAACGGGTAAAAGGCCCAATGACTCCTCTTTCGGTGAGAACAAG GACATGGTCAAGTGGGTGTTAGAGGTTGCAATATCGTCTAAAAAAGATGAAGGAAGTGGCCGTGTCACGGGCAGCAATGGTATTCTT GATTTGAACCAGCTAGTCGACCAGAGAATGAATCCGTCTGCAAGCAATTATGCAGAGATTAAAAAGGTTTTTGATGTGGCTTTGCTT TGCACTTCTTCGCTGCCCATTAATAGGCCATCCATGAGAAGAGTTGTTGAATTATTGAAGGATAACAGCGTTGCTCGTTCTAAGTCA ATCCGATAG
peptide	MEHMKLQFLLLIQLFLFIIPASCLNRDIAILLRVKTGQLGDPNGLLSDWNASAPNAPCNWTGITCDRKTRKVVSIEFTSFGISGHFP ADFCRISTLKKLNVGDNSFGDSISSDSWSLCSHLHFLNLSLNFFVGKLPEFIAKFDNLTVLDVNSNNFSGDIPASLGRLPRLQELDI ANNLLNGSVPEFLSNLTELTRLVIAQNPFKPSPLPSSIGRLGKLRILYARFANLIGNIPDSIKDLKSIQNFDVAINNLTGKIPEIIG ELKTVEQIELFQNKFSGELPNTFSGLVSLFRFDASQNNLTGKIPDSLARLPLVSLNLNDNNLEGEIPESLSLNPNLTQFKLFNNSFS GILPQDFGLSSDLDEFDVSGNNLEGSLPPNLCSRKKLRILNLFDNRFSGSIPESYGECNSLTYVRVYNNQFSGEIPTGFWSFAGYTF LELRNNNFQGSIPASISNARGLTEILISSNKFSGELPAEICNLEEIVIMNISKNQLSGELPWCITKLKTLQKFDLSENRITGQIPKS VSSWTDLTELNLANNQLTGEIPGELGTLPVLTYLDLAGNSLSGEIPSELSNLKLIKFNVSNNRLEGKVPLVFDNDFFVSGLQGNPDL CSPDLKPLPECPRSKSVSLYLVCILSALAVILVGSLVWVLIKAKRLLPIRSKRKSAWRITAFQRVGFTEGDLLASLTNDNLIGAGGS GRVYRVKLKNGQMVAVKKLWEAKRERESEEVFRSEVETLGRVRHGNIVKLLYSGIGDDFRILVYEYMENGSLGDVLHGEKGGILLDW PRRFAIAVGAAHGLAYLHHDSLPAIVHRDVKSNNILLDEDFRPKVADFGLAKVMQQDSEESDQVMSHIAGSYGYIAPEYAYTLKINE KSDVYSFGVLLLELITGKRPNDSSFGENKDMVKWVLEVAISSKKDEGSGRVTGSNGILDLNQLVDQRMNPSASNYAEIKKVFDVALL CTSSLPINRPSMRRVVELLKDNSVARSKSIR
Gene start	84701
Gene end	88400
Strand	1

Nicotiana benthamiana IDA-like and *HAE*-like gene families

Gene name	NbenIDA1A
SolGenomics source	N.benthamiana Genome v1.0.1
SolGenomics sequence ID	–

SolGenomics scaffold	Niben101Scf00570
CDS	ATGGCTTCCTCCTCCTCTTCCTCTTCTTCTTCTAAAAATAAAACCCCTTTTTACTTAATTTGTTTGATTCTTGCCATTTCTTTTCTT GTTGGTTATGGAGTTGAAGCAAGACCAGGAAGAATGATAAAGGAGGAAGAAGAAGCCAATTCAAGAATATTTTCAACACAACATTTG AAGGCATACAGAAAAGAAAATGCATACAAAACAGAAAATTTGGTATTTACTATGCTACCAAAAGGGGTTCCAATTCCTCCTTCTGCT CCATCTAAG
peptide	MASSSSSSSSKNKTPFYLICLILAISFLVGYGVEARPGRMIKEEEEANSRIFSTQHLKAYRKENAYKTENLVFTMLPKGVPIPPSA PSK
Gene start	62104
Gene end	62373
Strand	-1
Gene name	NbenIDA1B
SolGenomics source	N.benthamiana Genome v1.0.1
SolGenomics sequence ID	–
SolGenomics scaffold	Niben101Scf01338
CDS	ATGGCCTCCTCCTCTTCCTCTTCTTTTTCTAAAAACAAAACCATTTATTATTTAATTTGCTTGATTCTTGCCATTTCTTTTCTTCTT GATTATGGAGTTGAAGCAAGACCAGGGAGAATGATAATGGAGGGAAAAAAAGCAAATTCAAGAATATTTTCAACACAACATTTGAAG GTATACAGAAAAGAAAATGCATACAAAACAGAAAATTTGGTATTTACTATGCTACCAAAAGGGGTTCCAATTCCTCCTTCTGCTCCA TCTAAGAGACACAATGCTTTTGTGGACTCTTCACCTCAAAATTGA
peptide	MASSSSSSFSKNKTIYYLICLILAISFLLDYGVEARPGRMIMEGKKANSRIFSTQHLKVYRKENAYKTENLVFTMLPKGVPIPPSAP SKRHNAFVDSSPQN*
Gene start	640730
Gene end	641035
Strand	1
Gene name	NbenIDA2A
SolGenomics source	N.benthamiana Genome v1.0.1
SolGenomics sequence ID	Niben101Scf23219g00003.1
SolGenomics scaffold	Niben101Scf23219
CDS	ATGGCTTATTCTACTAATTCTAAAACTTTTTATTTTTCATGGAATTTTATGTGCTTGATTCTTACCCTTTCTCTTGTTCTTGGCTAT GGTGCTGCAGTGAGATCAATGGTGGCAACGACGACGACGAAGAATAAAGAGGAAGCTTCTGGAATGTTCTCAGAGCCTGTGAAAGAC TTATACGGTGAAAATGAATATTTGAAAGGTGATTGGCTCAATATGCTACCAAAAGGTGTTCCTATTCCTCCTTCTGCACCATCCAAA AGGCACAATTATTATGTGAACTCTTACCCTTAA
peptide	MAYSTNSKTFHFSWNFICLILTLSLVLGFSAAVRSMVTTTATTTTKGEASGMFSEPVKDFYGEKNLKENWFNMLPKGVPIPPSAPSK RHNYYVNPYP*
Gene start	7370
Gene end	7663
Strand	-1
Gene name	NbenIDA2B
SolGenomics source	N.benthamiana Genome v1.0.1
SolGenomics sequence ID	Niben101Scf03368g01013.1
SolGenomics scaffold	Niben101Scf03368
CDS	ATGGCTTATTCTACTAATTCTAAAACCTTTCATTTTTCATGGAATTTCATTTGCTTGATTCTTACCCTTTCTCTTGTTCTTGGCTTT AGTGCTGCAGTGAGATCAATGGTGACAACAACAGCGACGACGACGACGAAAGGAGAAGCTTCTGGAATGTTCTCAGAGCCCGTGAAA GACTTCTATGGTGAAAAGAATCTGAAAGAAAATTGGTTCAATATGCTACCAAAAGGTGTTCCTATTCCTCCTTCTGCACCATCCAAA AGGCACAATTATTATGTGAACCCTTACCCTTAA
peptide	MAYSTNSKTFYFSWNFMCLILTLSLVLGYGAAVRSMVATTTTKNKEEASGMFSEPVKDLYGENEYLKGDWLNMLPKGVPIPPSAPSK RHNYYVNSYP*
Gene start	114599
Gene end	114892

Strand	-1
Gene name	NbenIDA3A
SolGenomics source	N.benthamiana Genome v1.0.1
SolGenomics sequence ID	–
SolGenomics scaffold	Niben101Scf18667
CDS	ATGTTGAAAAGGTTTAAAAACACAACAATATTAGTCTTGCTACTTTCTCTTCATCTTCTTCTGATTTTCTTGGCTGATTATCACCAT GCAAATGCAACAAAGAACTCACAACTTTTTAATGTTAAGCCTTTGCCTAATTCTCACAATAATTCTCCTCATACATCATTTTCTCAA TCTTTGCCAAAAGGAATCCCTATTCCACCTTCTGCTCCTTCCAAAAGGCACAATGGTATCAACCTCTAA
peptide	MLKRFKNTTILVLLLSLHLLLIFLADYHHANATKNSQLFNVKPLPNSHNNSPHTSFSQSLPKGIPIPPSAPSKRHNGINL*
Gene start	206436
Gene end	206678
Strand	1
Gene name	NbenIDA3B
SolGenomics source	N.benthamiana Genome v1.0.1
SolGenomics sequence ID	–
SolGenomics scaffold	Niben101Scf01180
CDS	ATGTTGAAAAGGTTTAAAAACAAAACAATATTAGTGTTGCTGCCATTTCTTCTTATTCTTCTGATATTTATGGCTGATAATTACCAT GCAAATGCAACAAAGAACTCACAAGTTTTTAATGTTAAGCCATTGCCTAATTCCCACAATAATTCTCCTCACAGATCATTTTCTCAG TCTTTGCCAAAAGGAATACCTGTTCCACCTTCTGCTCCTTCGAAAAGGCACAATGGTATCAACCTCTAA
peptide	MLKRFKNKTILVLLPFLLILLIFMADNYHANATKNSQVFNVKPLPNSHNNSPHRSFSQSLPKGIPVPPSAPSKRHNGINL*
Gene start	267334
Gene end	267576
Strand	-1
Gene name	NbenIDA4
SolGenomics source	N.benthamiana Genome v1.0.1
SolGenomics sequence ID	–
SolGenomics scaffold	Niben101Scf19133
CDS	ATGGGGAAAATGAGCTTAAAGACAACAATACTATTTGTTGTTTTGCTTCTTTTGATGGTTGACCATGCTTATGCTGCAAGGGCAACG CACACACAATTTCTCAAAGTTCAGCCTTTGCATATGATGAATAAATCTCATCAATTCTCAGAGTCTTTGCCAAAAGGGGTCCCAATT CCACCTTCTGCTCCTTCCCAACGGCACAATGGTATCAACCTCAAAAGGCTAATTATTAGGCCTTGA
peptide	MGKMSLKTTILFVVLLLLMVDHAYAARATHTQFLKVQPLHMMNKSHQFSESLPKGVPIPPSAPSQRHNGINLKRLIIRP*
Gene start	87532
Gene end	87771
Strand	1
Gene name	NbenIDA5A
SolGenomics source	N.benthamiana Genome v1.0.1
SolGenomics sequence ID	–
SolGenomics scaffold	Niben101Scf03848
CDS	ATGATCAGTTTCTTCAGAAGAAAAGTAGCTCTTATTCTAGTCTTTTGGATGGCTATTATATTAATCACTATTTTTGGTCATTGTCAT GGTTCAAGAAGCAGCTCTCAAGTATTTAACCCAAGTAGCCAAAGAAACTCTCATCGATATGGCCATTTTTGGAACTTACTGCCTAAA AGAATTCCAATACCAGCTTCTGGTCCATCAAGAAAACACAATGATATTGGTCTTAAGAGTACTTGGAGATTACCCTAA
peptide	MISFFRRKVALILVFWMAIILITIFGHCHGSRSSSQVFNPSSQRNSHRYGHFWNLLPKRIPIPASGPSRKHNDIGLKSTWRLP*

Gene start	699324
Gene end	699575
Strand	1
Gene name	NbenIDA5B
SolGenomics source	N.benthamiana Genome v1.0.1
SolGenomics sequence ID	–
SolGenomics scaffold	Niben101Scf02135
CDS	ATGATTAGTTTCTTCAGAAGAAAAGTACCTCTTATTCTAGTCTTTATATTAATCACTATTTTTGGTCATTGTCATGGTTCAAGAAGC AGCTCTCAAAAATTTAACCCGAGTAGCCAAAGAAATTCTCATCAATATGGCCATTTTTGGAACTTGTTGCCAAAGAGAATTCCAATA CCAGCTTCTGGTCCATCAAGAAAACATAATGATATTGGTCTTAAGAGTACTTGGAGATTACCCTGA
peptide	MISFFRRKVPLILVFILITIFGHCHGSRSSSQKFNPSSQRNSHQYGHFWNLLPKRIPIPASGPSRKHNDIGLKSTWRLP*
Gene start	404883
Gene end	405122
Strand	-1
Gene name	NbenHAE.1
SolGenomics source	N.benthamiana Genome v1.0.1
SolGenomics sequence ID	Niben101Scf09774g00001.1
SolGenomics scaffold	Niben101Scf09774Ctg001
CDS	ATGGGCTATATCTGCAAAGACTGAAACTTTCTCTTTCCGACACAGAAGGTGCATTTTCTTCTTGGTCTGAACATGATCTTACCCCCT GTAACTGGACAGGTGTCACCTGTAACGACGCGCCGTCTCCCTCCGTCATCGCCGTTAATCTCTCCGGCGCTTCTCTAGCCGGACCCT TCCCTATATTCCTCTGCCACCTCACTTCACTTTCATCCCTCTCTCTTTCCAATAATCTTTTAAATTCTAGTCTCCCTCTTTCTATTT CTGAATGTCGTAGCCTCACTTACCTTGACCTTTCTCAGAATCTCCTCGGCGGCCCTATTCCTGAAACAATTGCTCATCTCCCTTACC TCAGATACCTTGATCTTAGCGGGTGCTATTTTACGGGAGATATTCCGGCAAGTTTCGGAAAATTCCAGCGACTGGAGACTCTTATAC TGACTGAAAATGTTCTTACCGGTAAAGTTCCTGCTACGTTAGGTAATGTAACGAGCCTCAGGACAATTGAACTCGCTTACAACCCAT TTGTACCGAGCCAGTTTCCCCCTGAACTTGGTAACTTGACGAATCTTGAGACATTATGGCTAAGTATGTGTAATCTTGTTGGTTCAA TTCCCCTTAGTATTGAGAAATTGAGTCAATTGACTAATTTTGATGTGTCCAATAATAGACTCGTTGGATCGATACCAAGTACAATTT TCCAGCTTAATAGTATTGTCCAAATTGAGCTGTACAATAATTCCCTTACTGGATTTTTGCCTAGTGGATGGTCTAACTTGACGAGAT TGAGAAGATTCGATGTGTCGACTAACAAGTTAAATGGGACTATTCCTGATGAGTTGTGTGAATTGTCACTTGAGTCACTCAATTTAT TTGAGAATCAATTTGATGGTTTATTTCCAGAAAGTATAGCTAAGTCTCCTAATTTATATGAGCTCAAGTTATTCTCTAACAGATTTT CAGGGTCATTGCCAAGTGAACTAGGCAAGAACTCAGCTTTACAGTATCTTGACGTTTCATACAACAAATTTTCGGGTAAATTTCCTG AAACTTTGTGTGAAATGCGAGCTTTAGAGGATCTTATAGCAATATACAATTCGTTCTCCGGGAATATTCCAGCTAGTCTTGGCAACT GCCGGAGTTTGAGACGTGTCAGGTTTCGGGGTAATCAGCTATATGGGGAAGTCCCTACTGAGTTTTGGAGTTTGCCTCAGGTTTATC TTTTAGACCTTTTTGGCAATGCATTTTCAGGGAATATATCACACATGATTTCTGGTGCCAAAAACTTGTCTAACTTACAAATTTCAA GAAACAGAATCTCAGGGGTTATACCTAGTGAAATAGGAAAATTGAAGAATTTAGTTGAGTTTTCCGCAAGTCATAATGAGCTAACGG GAGAAATTCCAGGCACACTAGTGCATCTAGGTCAGTTAGGAACTCTTGATCTTAGTTTCAATGAGTTATCAGGGGAAATCCCCTTGG GAATTCACACAATGAAGCAAATCAGTGAGCTTAACTTGGCTAACAATGGGTTTTCGGGGAAAATTCCAGATGAAATTGGGACTTTGC CAGTGCTTAATTATCTTGATCTTTCTGGGAATTACTTCTCGGGTGCAATTCCACTCAGCTTGCAAAGCCTGAAGCTTAATAAGCTAA ATTTGTCAAGTAATCGGCTGTCGGGGACTGTTCCTGCATTTTTTGATAAAGGTGTTTATAGAAATAGCTTTTCAGGAAACCCAAGTT TGTGTCAAGGTGTTGCTGGTCTTTGTACTGCAAAAGGTAGAGGAAAGCGTGAACGATACCTGTGGGCGTTGAGATCTATCTACACAG TTGCTGGCTTTGTTTTTCTTGTCGGGATTGCTATGTTCATTTGGAAGTACCAGAAATTCAAGAAAATTAAGAAAGGAATCAGTATTT CAAAGTGGACATCATTCCATAAGCTCGGATTCAGTGAATTTGAAATACTTTATGGCCTAGATGAAGCTAATGTAATAGGAAATGGAG CTTCAGGAAGAGTTTACAAAGCTGTTCTAAGCAATGGTGAAGCAGTAGCAGTTAAGAAGCTATGGGAGAGATCAGTTAAAGATGAAA CCAGTTTCGGTGCTCTTGAGTCTAATAAAGACGAGTTTGAAATGGAAGTTGAAACTCTGGGTAAAATTAGGCACAAGAATATTGTGA GATTGTGGTGCTGTTGTGATACTGGGGGTAGCAAGCTTTTGGTATATGAGTACATGCCAAATGGAAGTTTGGGTGATTTGCTGCACA GTTGCAATGCCAAATTGTTGGATTGGCCGTTGAGGTTCAAGATAGCTTTGGATGCTGCTGAGGGGCTCTCTTATTTACACCATGATT GTGTTCCTCCAATTGTTCACCGAGATGTTAAGTCAAACAACATATTACTGGATGGTGAATTTGGAGCCAAAATATCAGATTTTGGTG TGGCAAAAATTGTTAAAGCAGCCAGCAAAGGTGGTGCGGAATCCATGTCTGTGATTGCTGGTTCCTGTGGTTACATTGCACCAGAGT ATGCATACACTCTTCATGTGAATGAAAAGAGCGACATTTATAGCTTTGGAGTGGTCATTTTGGAGCTGGTGACAGGTAAAAGACCAG TTGGTCCAGAGTTTGGGGAGAAAGATCTAGCTACTTGGGTACGCACCACCTTGAACGAGAAAGGAGTTGATCAGTTGCTCGACCCAA ATTTGAATTCCAACTTCAAAGAACATATATGCAAGCTTCTTGATATTGGTCTATGTTGTCTTAACCACATTCCAGCTAATCGCCCCT CAATGCGCAGAGTGGTGAAAATGCTCCAAGAATCAGTTCCTTACAATGTGCCAGGGATGGTAAACAAGAATGGTAAACTTCTCCCTT ACTTTTTTCCGAAATCAGTCTAG
peptide	MQLFIFFLSSLPFIFALNQDGLYLQRLKLSLSDTEGAFSSWSEHDLTPCNWTGVTCNDAPSPSVIAVNLSGASLAGPFPIFLCHLTS LSSLSLSNNLLNSSLPLSISECRSLTYLDLSQNLLGGPIPETIAHLPYLRYLDLSGCYFTGDIPASFGKFQRLETLILTENVLTGKV PATLGNVTSLRTIELAYNPFVPSQFPPELGNLTNLETLWLSMCNLVGSIPLSIEKLSQLTNFDVSNNRLVGSIPSTIFQLNSIVQIE LYNNSLTGFLPSGWSNLTRLRRFDVSTNKLNGTIPDELCELSLESLNLFENQFDGLFPESIAKSPNLYELKLFSNRFSGSLPSELGK NSALQYLDVSYNKFSGKFPETLCEMRALEDLIAIYNSFSGNIPASLGNCRSLRRVRFRGNQLYGEVPTEFWSLPQVYLLDLFGNAFS

	GNISHMISGAKNLSNLQISRNRISGVIPSEIGKLKNLVEFSASHNELTGEIPGTLVHLGQLGTLDLSFNELSGEIPLGIHTMKQISE LNLANNGFSGKIPDEIGTLPVLNYLDLSGNYFSGAIPLSLQSLKLNKLNLSSNRLSGTVPAFFDKGVYRNSFSGNPSLCQGVAGLCT AKGRGKRERYLWALRSIYTVAGFVFLVGIAMFIWKYQKFKKIKKGISISKWTSFHKLGFSEFEILYGLDEANVIGNGASGRVYKAVL SNGEAVAVKKLWERSVKDETSFGALESNKDEFEMEVETLGKIRHKNIVRLWCCCDTGGSKLLVYEYMPNGSLGDLLHSCNAKLLDWP LRFKIALDAAEGLSYLHHDCVPPIVHRDVKSNNILLDGEFGAKISDFGVAKIVKAASKGGAESMSVIAGSCGYIAPEYAYTLHVNEK SDIYSFGVVILELVTGKRPVGPEFGEKDLATWVRTTLNEKGVDQLLDPNLNSNFKEHICKLLDIGLCCLNHIPANRPSMRRVVKMLQ ESVPYNVPGMVNKNGKLLPYFFPKSV
Gene start	1101
Gene end	4300
Strand	1
Gene name	NbenHAE.2
SolGenomics source	N.benthamiana Genome v1.0.1
SolGenomics sequence ID	Niben101Scf05190g00001.1
SolGenomics scaffold	Niben101Scf05190Ctg007
CDS	ATGCAATTATTCATCTTCTTTTTGAGTACTCTGCCTTTGATATTTGCTTTAAATCAAGATGGGCTATATTTGCAAAGACTGAAACTT TCTCTTTCCGATACAGGAGGTGCATTTTCTTCTTGGTCCGAACATGATCTTACCCCCTGTAACTGGACAGGTGTCACTTGTAACGAT GCGCCGTCTCCCTCCGTTGTCGCCGTTAATCTCTCCGGCGCTTCTCTCGCCGGACCTTTCCCCATTTTCCTCTGCCACCTCCCTTTG CTTTCATCCCTCTCTCTTTCCAATAATCTCATAAACTCTACTCTTCCACTTTCTATTTCGGAATGTCGTAGCCTCACTTACCTTGAC CTTTCTCAGAATCTCCTCGATACCTTGATCTTAGCGGGTGCTATTTTACTGGGGATATACCGGAAACAACTGGAAACTCTTATACTT ACTGAAAATGTTCTTACTGGTAAAGTTCCTGCTATGTTAGGTAATGTAACGAGTCTCAGGACAATTGAACTCGCTTACAACCCATTT TCACCGAGTCAGTTTCCTCCTGAACTCGGTAACTTGACGAATCTTGAGACATTATGGCTAAGTATGTGTAATCTTGTTGGTTCAATT CCACAAAGTATCGAGAAATTGAGTCGATTGGCTAATTTTGATGTGTCTAATAATAGACTCGTTGGATCGATACCAAGTACAATTTTC CAGCTTAGTAGTATTGTCCAAATTGAGCTGTACAATAATTCCCTTACTGGATTTTTGCCTAGTGGATGGTCTAACCTGACAAAATTG AGAAGATTCGATGTCTCAACTAACAAGTTTACTGGTACTATTCCTGATGAGTTGTGTGATTTGTCACTTGAGTCACTCAACTTATTT GAGAATCAATTTGATGGTTTATTTCCAGAAAGTATAGCTAAGTCTCCTAATTTGTATGAGCTCAAGTTATTCTCTAACAGATTTTCA GGGTCACTGCCTAGTGAACTAGGAAAGAACTCAGCTTTACAGTATCTTGATGTTTCATACAACAAATTTTCTGGTAAAATTCCAGAA AGTCTGTGTGAAATGGGAGCTTTAGAGGATCTTATAATGATATATAATTCGTTCTCCGGGACTATTCCGGCTAGTCTTGGTAACTGC CGGAGTTTGAGACGTGTCAGGTTTCGGGGTAATCAGCTATATGGGGAAGTCCCTACTGAGTTTTGGAGTTTGCCTCAGCTATATGGG GAAGTCCCTACTGAGTTTTGGAGTTTGCCTCAGGTTTATCTTTTAGACCTTTTTGGCAATGCATTTTCAGGAAATATATCACACATG ATTGCTGGTGCAAAAAATTTGTCTAACTTACAAATATCAAGAAACAGAATCTCAGGGGTTATACCTAGTGAAGTAGGAAAATTGAAG AATTTAGTTGAGTTTTCCGCGAATCATAATGAGCTAACGGGAGAAATTCCAGGCAGATTAGTGTATCTAGGTCAGTTAGGAACCCTG GATCTTAGTTTCAATGAGTTATCAGGGGAAATCCCCTTGGGAATTCACTCAATGAAGCAACTCAGTGAGCTTAACTTGGCTAGCAAT GGGTTTTCAGGGAAAATTCCAGATGAAATTGGGACTTTGCCAGTGCTTAATTATCTTGATCTTTCTGGGAATTACTTCTCAGGTGAA ATCCCACTCAGTCTGCAAAGCTTGAAGCTTAATAAGCTAAATTTGTCTAATAATCGTCTGTCAGGGACTGTTCCTACATTTTTCGAT AAAGGTGTTTATAGAAATAGCTTTTTAGGAAACCCAAGTTTGTGTCAAGGTGTTGCTGGTCTTTGTACTGCTAAAGGTGGAGGAAAG CTTGACAGATACTTGTGGGCTTTGAGAGCTATCTATACAGTTGCTGGCTGTGTTTTTCTTGTTGGAATTGCTATATTCATTTGGAAG TACCAGAAATTCAAGAAAATTAAGAAAGGAATCACTATATCAAAGTGGACATCATTCCATAAGCTCGGATTCAGTGAATTCGAAATA CCTGCTGGCCTAGATGAAGCTAATGTAATTGGAAATGGAGCTTCAGGAAGAGTTTACAAAGCTGTCCTAAGCAATGGTGAGGCGGTA GCAGTTAAGAAGCTATGGGAGAGATCAGTTAAAGATGAAACCAGTTTTGGCGCTCTTGAGTCTGATAAAGACGAGTTTGAAATGGAA GTTGAAACTCTGGGTAAAATTAGGCACAAGAATATTGTGAGATTATGGTGCTGTTGTGATACTGGGGATAGCAAGCTCTTGGTGTAT GAGTACATGCCGAATGGAAGTTTGGGCGATTTGCTGAACAGTTGCAAGGCCAAATTGTTGGATTGGCCGTTGAGATTCAAGATAGCT TTAGATGCAGCTGAGGGGCTCTCTTATTTGCACCATGATTGTGTTCCTCCAATTGTACACCGCGATGTTAAGTCAAACAACATATTA CTGGATGGTGAGTTTGGAGCCAAAATTTCAGATTTTGGTGTGGCAAAAATTGTTAAAGCAGCCAGCAAAGGTGGTGTCGAATCCATG TCTGTAATTGCTGGTTCCTGTGGTTATATTGCACCAGAGTATGCATATACTCTTCATGTGAATGAAAAGAGCGACATTTATAGCTTT GGAGTGGTCATTTTGGAGCTGGTGACAGGACGAAGGCCTGTTGGTCCAGGATTTGGACAGAAAGATCTAGCTACTTGGGTACGCATG ACCTTGAACGAGAAAGGAGTTGATCAGTTGCTCGACCCCAATTTAAATTCCTGCTTCAAAAAACATATAAGCAAGGTTCTTGACATC GGTCTATGTTGTCTTAACCATGTTCCAACTAATCGCCCCTCAATGCGCAGAGTGGTGAAAATGCTCCAAGAATCAGTTCCTTATAAT GTGCCAGAGATGGTAAATAAGAATGGTAAATTTTCCCTTAGCTTTTTTCCAAAGTCAGTCTAG
peptide	MQLFIFFLSTLPLIFALNQDGLYLQRLKLSLSDTGGAFSSWSEHDLTPCNWTGVTCNDAPSPSVVAVNLSGASLAGPFPIFLCHLPL LSSLSLSNNLINSTLPLSISECRSLTYLDLSQNLLDTLILAGAILLGIYRKQLETLILTENVLTGKVPAMLGNVTSLRTIELAYNPF SPSQFPPELGNLTNLETLWLSMCNLVGSIPQSIEKLSRLANFDVSNNRLVGSIPSTIFQLSSIVQIELYNNSLTGFLPSGWSNLTKL RRFDVSTNKFTGTIPDELCDLSLESLNLFENQFDGLFPESIAKSPNLYELKLFSNRFSGSLPSELGKNSALQYLDVSYNKFSGKIPE SLCEMGALEDLIMIYNSFSGTIPASLGNCRSLRRVRFRGNQLYGEVPTEFWSLPQLYGEVPTEFWSLPQVYLLDLFGNAFSGNISHM IAGAKNLSNLQISRNRISGVIPSEVGKLKNLVEFSANHNELTGEIPGRLVYLGQLGTLDLSFNELSGEIPLGIHSMKQLSELNLASN GFSGKIPDEIGTLPVLNYLDLSGNYFSGEIPLSLQSLKLNKLNLSNNRLSGTVPTFFDKGVYRNSFLGNPSLCQGVAGLCTAKGGGK LDRYLWALRAIYTVAGCVFLVGIAIFIWKYQKFKKIKKGITISKWTSFHKLGFSEFEIPAGLDEANVIGNGASGRVYKAVLSNGEAV AVKKLWERSVKDETSFGALESDKDEFEMEVETLGKIRHKNIVRLWCCCDTGDSKLLVYEYMPNGSLGDLLNSCKAKLLDWPLRFKIA LDAAEGLSYLHHDCVPPIVHRDVKSNNILLDGEFGAKISDFGVAKIVKAASKGGVESMSVIAGSCGYIAPEYAYTLHVNEKSDIYSF GVVILELVTGRRPVGPGFGQKDLATWVRMTLNEKGVDQLLDPNLNSCFKKHISKVLDIGLCCLNHVPTNRPSMRRVVKMLQESVPYN VPEMVNKNGKFSLSFFPKSV
Gene start	1
Gene end	2400
Strand	1

Gene name	NbenHSL1.1
SolGenomics source	N.benthamiana Genome v1.0.1
SolGenomics sequence ID	Niben101Scf03169g02005.1
SolGenomics scaffold	Niben101Scf03169Ctg027
CDS	ATGTTTCTTCAAATCTTTGTTACCCTTTTATTCCCAACTTTGATTTTCTCACTTAACCAAGAGGGTCTGTATTTACACAACGTGAAG CTCGGATTTGATGACCCTGATAATGTTCTTTCCAACTGGAATGATCACGACGAGACACCATGTAACTGGTTTGGCATAACCTGTGAT CAAACAACTCGGTCCGTTACATCCTTGGACCTCGCTAATGCTAACGTTGCTGGTCCTTTTCCCTCACTTCTCTGTCGGTTAAAGAAA CTCCGCTACATTTCATTATACAATAACGCTATTAACTCCACTCTTCCTGAAGATTTCTCTGGGTGTGAATCTTTGGAACATCTAGAT TTGGCTCAGAATTTTTTGGTCGGTACACTTCCGTCGAGTTTACCTGAGCTTCCAAATTTGAAATACCTTGACTTGGGGGGAAACAAC TTTACCGGCGACATTCCGTCAAGTTTCGGTTCTTTCCGGCAGCTGGAGGTTCTTGGACTGGTTGGAAACTTGCTTGACGGGACTATT CCAGCGTTTCTGGGTAACATTTCAACGTTAAAGCAGCTGAATCTGTCGTACAACCCGTTTTCGACGGGTCAGATCCTTCCGGAGCTG GGAAATCTGACAAATCTCGAGGTTTTGTGGCTCTCGGACTGTAATTTGGTCGGTGAAGTTCCTGATACATTGGGCTGGTTGACGAAG ATTGTGGATTTGGACCTTGCTGTGAACTACTTGGACGGGCCGATCCCGAGTTGGCTCACTGAGTTAACTAGTGTTGAACAAATTGAG CTGTATAATAACTCGTTCACCGGCGAGTTACCAGTGAATGGGTGGTCGAAAATGACGGCGTTAAGGCGACTCGACGTGTCCATGAAT CGGGTCACGGGTACGGTTCCTAGGGAGTTGTGTGAGTTGCCACTCGAGTCGCTGAATCTTTATGAGAACCAAATGTTCGGTGAATTG CCACAAGGCATTGCGAATTCGCCGAATTTGTATGAGTTGCGGCTTTTTCACAACCGTTTCAATGGGAGTTTGCCTAATGATCTTGGG AAGAATTCGCCTTTGTTGTGGATTGATGTGTCTGAGAATAAATTTTCCGGTGAAATTCCGGAAAATTTATGTGGGAAAGGGTTTTTA GAGGAGCTTTTGATGATAGATAACTTACTTACTGGGGAAATTCCGGCGAGTTTGAGTGAATGCCGGAGCTTACTGCGGGTGAGATTG GCTCACAATCAGTTATCTGGTGATGTACCGGCGGGGTTCTGGGGCCTACCACACCTTTCCCTGCTTGAGCTCATGGACAATTCACTA TCTGGCGATATTGCGAAAACTATAGCCAGCGCTTCAAATTTATCAGCTTTGATTTTGTCCAAGAACAAATTTTCAGGTCCCATTCCG GAGGAGATTGGTTCTCTGGAAAATCTTCTTGATTTTGTGGGCAATGATAACCTGTTTTCTGGGCCTTTGCCGGCTAGTTTAGTGATG CTTGGACAATTGGGAAGGCTGGATCTTCACAATAATGAGTTAATTGGTGAGCTTCCAAGTGGGATTCATTCTTTGAAGAAGTTGAAT GAATTGAACTTGGCAAATAATGATCTTTCTGGAGCTATTCCCAAGGAAATTGGGAGCTTGTCTGTGTTGAATTATCTTGATCTATCA GGAAACCAGTTTTCAGGGAAGATCCCAATGGAGTTGCAGAATTTGAAGCTCAATCAGCTGAACTTGTCGAACAATGACCTTTCGGGT GATATCCCCCCGTTGTATGCAAAGGAAATGTACAAGAGTAGCTTTTTCGGGAACGCTGGTTTATGTGGAGACATTGAGGGCTTGTGT GAAGGAACAGCTGAAGGTAAAACTGCTGGTTATGTTTGGTTATTGAGGTTACTCTTTACTCTTGCTGGATTGGTGTTTGTAGTTGGG GTGGTTTGGTTCTATTGGAAGTATAAGAATTTTAAGAAAGCTAAAATGGCTATTGATAAGTCTAAATGGACTTTGATGTCGTTTCAT AAGTTAGGTTTCAATGAGTATGAAATCTTGGATGCTCTTGATGAGGACAACTTAATTGGAAGTGGCGCTTCTGGGAAGGTTTACAAG GTTGTTCTGAGCAAGGGTGACACTGTTGCGGTGAAGAAGATTTTGAGAAACACGAAAATAACAGATGAGAGTAGTGATATCGAGAAG GGTAGCATTCAAGATGATGGATTTGAAGCGGAGGTTGAGACATTGGGGAAGATACGGCACAAGAACATTGTTAAGCTATGGTGTTGT TGTACAACAAGGGATTGCAAACTTCTGGTTTACGAGTACATGCCTAATGGAAGCTTGGGTGATTTGCTGCACAGCAGCAAAAGCGGC CTTCTAGACTGGCCTATGAGATATAAGATAGCCATGGATGCTGCTGAGGGACTCTCTTACTTGCATCATGACTGTGCTCCGCCGATT GTTCACAGAGATGTTAAGTCAAACAACATCTTGTTGGATGGTGATTTTGGAGCCCGAGTTGCTGATTTTGGTGTAGCAAAGGCGGTC GATGCCAATGCCAAGGGAATCAAGTCCATGTCTGTCATTGCAGGGTCTTGTGGTTACATTGCTCCAGAATATGCATATACACTGCGG GTGAACGAGAAGAGTGATATATACAGCTTCGGAGTGGTAATTCTAGAGCTTGTGACTGGGAAGCGCCCCGTGGATCCTGAGTTTGGG GAAAAGGATTTGGTGAAGTGGGTATGCTCTACAATGGACCAGAAGGGTGTAGATCATGTTATTGATCCTAAACATGATTCTTGTTTC AAGGAGGAGATATGCAAGGTCTTAAATATTGGCCTCCTCTGCACTAGCCCTCTCCCAATCAACCGACCCTCGATGAGACGGGTTGTA AAAATGTTGCAAGAAGTGGGTGCTGGGAACCTGTCCAAGGCTGCCTCTAAGGATGGCAAATTGACTCCTTATTACTATGAAGAAGCA TCAGATCAAGGAAGTGTAGCTTAA
peptide	MFLQIFVTLLFPTLIFSLNQEGLYLHNVKLGFDDPDNVLSNWNEHDETPCNWFGITCDQTTRSVTSLDLANANVAGPLPSLLCRLKK LRYISLYNNAVNSTLPEDFSGCESLEHLDLAQNFLVGTLPSSLPELPNLKYLDLGGNNFTGDIPSSFGSFRQLEVLGLVGNLLDGTI PAFLGNISTLKQLNLSYNPFSTGQILPELGNLTNLEVLWLSDCNLVGEVPDTLGWLTKIVDLDLAVNYLDGPIPSWLTELTSVEQIE LYNNSFTGELPVNGWSKMTALRRLDVSMNRVTGTVPRELCELPLESLNLYENQMFGELPQGIANSPNLYELRLFHNRFNGSLPNDLG KNSPLLWIDVSENKFSGEIPENLCGKGFLEELLMIDNLLTGEIPASLSECRSLLRVRLAHNQLSGDVPAGFWGLPHLSLLELMDNSL SGDIAKTIASASNLSALILSKNKFSGPIPEEIGSLENLLDFVGNDNLFSGPLPASLVMLGQLGRLDLHNNELIGELPSGIHSLKKLN ELNLANNDLSGAIPKEIGSLSVLNYLDLSGNQFSGKIPMELQNLKLNQLNLSNNDLSGDIPPLYAKEMYKSSFFGNAGLCGDIEGLC EGTAEGKTAGYVWLLRLLFTLAGLVFVVGVVWFYWKYKNFKKAKMAIDKSKWTLMSFHKLGFNEYEILDALDEDNLIGSGASGKVYK VVLSKGDTVAVKKILRNTKITDESSDIEKGSIQDDGFEAEVETLGKIRHKNIVKLWCCCTTRDCKLLVYEYMPNGSLGDLLHSSKSG LLDWPMRYKIAMDAAEGLSYLHHDCAPPIVHRDVKSNNILLDGDFGARVADFGVAKAVDANAKGIKSMSVIAGSCGYIAPEYAYTLR VNEKSDIYSFGVVILELVTGKRPVDPEFGEKDLVKWVCSTMDQKGVDHVIDPKHDSCFKEEICKVLNIGLLCTSPLPINRPSMRRVV KMLQEVGAGNLSKAASKDGKLTPYYYEEASDQGSVA
Gene start	801
Gene end	3900
Strand	1
Gene name	NbenHSL1.2
SolGenomics source	N.benthamiana Genome v1.0.1
SolGenomics sequence ID	Niben101Scf11552g02006.1
SolGenomics scaffold	Niben101Scf11552Ctg025
CDS	ATGTTTCTTCAAATCTTTGTTACTCTTTTATTCCCAACTTTGATTTTCTCACTTAACCAAGAGGGTCTGTATTTACACAACGTGAAG CTCGGATTTGATGACCCTGATAATGTTCTTTCCAACTGGAATGAGCACGATGAGACACCGTGTAACTGGTTTGGCATAACCTGTGAT

	CAAACAACTCGGTCCGTTACATCCTTGGACCTCGCTAATGCTAACGTTGCTGGTCCTTTGCCTTCACTTCTCTGTCGGTTGAAGAAA CTGCGTTACATTTCGTTATACAATAACGCTGTTAACTCCACCCTTCCTGAAGATTTCTCCGGGTGTGAATCTTTGGAGCATCTCGAT TTGGCTCAGAATTTTTTGGTCGGTACACTTCCGGCGAGTTTACCTGAGCTTCCGAATTTGAAATACCTTGACTTGGGGGGAAACAAC TTTACCGGCGACATTCCTTCAAGTTTCGGTTCTTTCCGGCAGCTGGAGGTTCTTGGACTGGTTGGGAACTTGCTTGACGGGACTATT CCAGCATTTCTGGGTAACATTTCGACGTTAAAGCAGCTGAATCTGTCGTACAACCCGTTTTCGACGGGTCGGATCCTTCCGGAGCTG GGAAATCTGACAAATCTCGAGGTTTTGTGGCTTTCCGACTGTAATTTGGTCGGTGAAGTTCCTGATACATTGGGTCGGTTGAAGAAT ATTGTGGATTTGGACCTTGCTGTGAACTACTTGGATGGACCGATCCCGAGTTGGCTCACTGAGTTAACTAGTGCTGAACAAATTGAG CTATATAACAACTCGTTCACCGGCGAGTTACCGGTGAGTGGGTGGTCGAAAATGACGGCGTTAAGGCGACTCGACGTGTCGATGAAT CGGGTCACGGGTCCCATTCCGGAGGAGATTGGTTCTCTGGAAAATCTTCTTGATTTTGTGGGCAATGATAACCTGTTTTCTGGGCCT TTGCCAGCTAGTTTAGTGATGCTTGGACAATTGGGAAGGCTGGATCTTCACAATAATGAGTTAATTGGTGAGCTTCCAAGTGGGATT CATTCTTTGAAGAAGTTGAATGAATTGAACTTGGCAAATAATGATCTTTCTGGAGCTATTCCCAAGGAAATTGGGAGCTTGTCTGTG TTGAATTATCTTGATCTATCAGGAAACCAGTTGTCAGGGAAGATCCCAATGGAGTTGCAGAATTTGAAGCTCAATCAGCTGAACTTG TCGAACAATGACCTTTCGGGTGATATCCCCCCGTTGTATGCAAAGGAAATGTACAAGAGTAGCTTTTTCGGGAACGCTGGTTTATGT GGAGACATTGAGGGCTTGTGTGAAGGAACAGCTGAAGGTAAAACTGCTGGTTATGTTTGGTTATTGAGGTTACTCTTTACTCTTGCT GGATTGGTGTTTGTAGTTGGGGTGGTTTGGTTCTATTGGAAGTATAAGAATTTTAAGAAAGCTAAAATGGCTATTGATAAGTCTAAA TGGACTTTGATGTCGTTTCATAAGTTAGGTTTCAATGAGTATGAAATCTTGGATGCTCTTGATGAGGACAACTTAATTGGAAGTGGC GCTTCAGGAAAGGTTTACAAGGTTGTTCTGAGCAAGGGTGACACTGTTGCGGTGAAAAAGATTTTGATAAGTGCGAAAATAACAGAT GAGAGTAGTGATATCGAGAAGGGTAGCATTCAAGATGGTTTTGAAGCTGAGGTTGAGACATTGGGGAAGATACGGCACAAGAACATT GTTAAGCTATGGTGTTGTTGCACAACAAGGGATTGCAAACTTCTGGTTTACGAGTACATGCCTAATGGAAGCTTGGGTGATTTGCTA CACAGCAGCAAAAGTGGCCTTCTAGACTGGCCTATGAGATATAAGATAGCCATGGATGCTGCTGAGGGGCTCTCTTACTTGCATCAT GACTGTGCTCCGCCTATTGTTCACAGAGATGTTAAGTCAAACAACATCTTGTTGGATGGTGATTTTGGAGCTCGAGTTGCTGATTTT GGCGTAGCAAAGGCGGTCGATGCCAATGCCAAGGGAATCAAGTCCATGTCTGCCATTGCAGGGTCTTGTGGTTACATTGCTCCAGAA TATGCATACACACTGCGGGTGAGTGAGAAGAGCGATATATACAGCTTCGGTGTGGTAATCCTAGAGCTTGTGACTGGGAAACGCCCC GTGGATCCTGAGTTCAGGGAAAAGGATTTGGTGAAGTGGGTATGCTTTACATTGGACCAGAAGGGTGTAGATCATGTAATTGACCCT AAACATGATTCTTGTTTCAAAGAGGAGATATGCAAGGTCTTAAACATCGGCCTCCTCTGTACTAGCCCTCTCCCTATTAACCGACCC TCGATGAGACGGGTTGTAAAAATGTTGCAAGAAGTGGGTGCTGGGAACCTGCCCAAGGCTGCTTCTAAGGATGGCAAATTGACTCCT TATTACTATGAAGAAGCTTCAGATCAAGGAAGTGTAGCCTAA
peptide	MFLQIFVTLLFPTLIFSLNQEGLYLHNVKLGFDDPDNVLSNWNEHDETPCNWFGITCDQTTRSVTSLDLANANVAGPLPSLLCRLKK LRYISLYNNAVNSTLPEDFSGCESLEHLDLAQNFLVGTLPASLPELPNLKYLDLGGNNFTGDIPSSFGSFRQLEVLGLVGNLLDGTI PAFLGNISTLKQLNLSYNPFSTGRILPELGNLTNLEVLWLSDCNLVGEVPDTLGRLKNIVDLDLAVNYLDGPIPSWLTELTSAEQIE LYNNSFTGELPVSGWSKMTALRRLDVSMNRVTGPIPEEIGSLENLLDFVGNDNLFSGPLPASLVMLGQLGRLDLHNNELIGELPSGI HSLKKLNELNLANNDLSGAIPKEIGSLSVLNYLDLSGNQLSGKIPMELQNLKLNQLNLSNNDLSGDIPPLYAKEMYKSSFFGNAGLC GDIEGLCEGTAEGKTAGYVWLLRLLFTLAGLVFVVGVVWFYWKYKNFKKAKMAIDKSKWTLMSFHKLGFNEYEILDALDEDNLIGSG ASGKVYKVVLSKGDTVAVKKILISAKITDESSDIEKGSIQDGFEAEVETLGKIRHKNIVKLWCCCTTRDCKLLVYEYMPNGSLGDLL HSSKSGLLDWPMRYKIAMDAAEGLSYLHHDCAPPIVHRDVKSNNILLDGDFGARVADFGVAKAVDANAKGIKSMSAIAGSCGYIAPE YAYTLRVSEKSDIYSFGVVILELVTGKRPVDPEFREKDLVKWVCFTLDQKGVDHVIDPKHDSCFKEEICKVLNIGLLCTSPLPINRP SMRRVVKMLQEVGAGNLPKAASKDGKLTPYYYEEASDQGSVA
Gene start	201
Gene end	1700
Strand	-1
Gene name	NbenHSL2.1
SolGenomics source	N.benthamiana Genome v1.0.1
SolGenomics sequence ID	Niben101Scf08143g03001.1
SolGenomics scaffold	Niben101Scf08143Ctg022
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	TGTAGTCCGGATCTTAAACCTCTGCCTCAATGCCCAAGACCCAAAAGTATAAGCTTGTATTTGGTGTGTATTTTATCAGCTTTAGCC GTCATACTTGTTGGGTCACTTGTTTGGGCCTTGATCAAGGCCAAAAAGTTGTTACCCATTCGGAGTAAGCGTAAAAGTGCATGGAGA ATTACTGCATTTCAACGGGTTGGATTCACGGAGGGAGACTTATTAGCTGCACTGATAAATGAGAATCTCATTGGTGCTGGTGGGTCT GGACGGGTATATAGGGTCAAACTAAAAACCGGGCAGATGGTCGCGGTGAAGAAGCTTTGGGAGGCTAAACGGGAGAGAGAATCCGAG GAGGTCTTCAGGACGGAGGTGGAGACTCTAGGGAGAGTCCGACATGGAAACATAGTAAAACTATTGTACAGTGGCATTGGTGATGAC TTCAGGATATTGGTGTATGAGTACATGGAGAATGGGAGCTTAGGAGACGTATTACACGGGGAAAAAGGTGGCATTCTTTTGGATTGG CCAAGGAGATTTGGCATAGCAGTTGGAGCAGCTCAAGGATTGGCCTATTTGCACCATGATTCTGTTCCTGCAATAGTACACAGAGAT GTCAAGTCTAATAACATTTTGTTGGACGAGGATTTTAGGCCAAAAGTTGCTGATTTTGGGCTAGCTAAGGTAATGCAGCAGGACAGT GAGGAGAGTGATCAAGTCATGTCCCATATTGCTGGTTCCTACGGCTACATTGCACCTGAATATGCCTATACTCTGAAGATTAATGAG AAGAGTGACGTCTATAGCTTTGGCGTGGTCCTGTTGGAACTAATAATCGGTAAAAGGCCCAATGACTCCTCTTTCGGTGAGAACAAG GACATGGTCAAGTGGGTGTTAGAGGTTGCAATATCGTCTAAGAAAGATGAAGGAAGTGGCCGTGTCACGGGCAGCAATAGTATTCTT GATTTGAACCGGCTAGTCGACCAGAGAATGAATCCGTCTGCAAGCAATTATGCAGAGATTAAAAAGGTTTTTGATGTGGCTTTGCTT TGCACTTCTTCATTGCCCATTAATAGGCCATCCATGAGAAGAGTTGTTGAATTGTTGAAGGATAACAATGTTGCTCGTTCTAAGTCA ATCCGATAG
peptide	MEHMKFQFLLLILLCLFIIPVSCLNRDIAILLRVKTGQLADPNGLLSDWNASAPNAPCSWTGITCDRKTHKVVSIEFPSFGISGHFP ADFCRISTLQKLNLGDNSFGDSISSDSWSLCSHLHFLNLSLNFFVGKLPEFIAKFDNLTILDVNSNNFSGDIPASLGRLPRLQELDI ANNLLNGSVPGFLSNLTELTRLVIAQNPFKPSPLPSSIGRLGKLRILYARFANLIGNIPDSIRDLKSIQNFDVAINNLTGKIPESIG ELKTVEQIELFQNRFSGELPNTFPGLVSLFRFDASQNNLTGKIPDSLARLPLVSLNLNDNNLEGEIPESLVLNPNLTQFKLFNNRFS GTLPQDFGLSSDLDEFDVSGNNLEGSLPPNLCSRKKLRILNLFDNRFSGSIPESYGECNSLTYVRVYNNQLSGELPTGFWSFAGYTF LELRNNNFQGSIPASISDARGLTEILISGNKFSGKLPAGLCNLEEIVIMDISKNQLSGELPSCITKLKTLQKLDLSENRITGQIPKL VSSWTDLTELNLANNQLTGEIPGELGTLPVLTYLDLARNSLSGEIPSELSNVKLNKFNVSNNRLEGKVPPVFDNDFFISGLQGNPDL CSPDLKPLPQCPRPKSISLYLVCILSALAVILVGSLVWALIKAKKLLPIRSKRKSAWRITAFQRVGFTEGDLLAALINENLIGAGGS GRVYRVKLKTGQMVAVKKLWEAKRERESEEVFRTEVETLGRVRHGNIVKLLYSGIGDDFRILVYEYMENGSLGDVLHGEKGGILLDW PRRFGIAVGAAQGLAYLHHDSVPAIVHRDVKSNNILLDEDFRPKVADFGLAKVMQQDSEESDQVMSHIAGSYGYIAPEYAYTLKINE KSDVYSFGVVLLELIIGKRPNDSSFGENKDMVKWVLEVAISSKKDEGSGRVTGSNSILDLNRLVDQRMNPSASNYAEIKKVFDVALL CTSSLPINRPSMRRVVELLKDNNVARSKSIR
Gene start	18001
Gene end	21800
Strand	1
Gene name	NbenHSL2.2
SolGenomics source	N.benthamiana Genome v1.0.1
SolGenomics sequence ID	Niben101Scf02417g01010.1
SolGenomics scaffold	Niben101Scf02417Ctg009
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	GATTTGAAGCAGCTAGTAGACCAGAGAATGAATCCGTCTGCAAGCAATTATGCAGAGATTAAAAAGGTTTTTGATGTGGCTTTGCTTTGCACTTCTTCATTGCCCATTAATAGGCCATCCATGAGAAGAGTTGTAGAATTGTTGAAGGATAACAGTGTTGCTCGTTCTAAGTCAATCCGATAG
peptide	MEHMKLHFMLLIQLFLFIIPASCLNRDIAILLRVKSGQLGDPNGLLSDWNASAPNAPCNWTGITCDRKTHKVVSIEFASFGISGHFPADFCRISTLQKLNLGDNSFGDSISSDSLSLCSHLHFLNLSLNFFVGKLPEFIAKFDSLTVLDVNSNNFSGDIPASLGRLPRLQELDISNNLLNGSVPEFLSNLTELTRLVIAQNPFKPSPLPPLIGRLGKLRILYARSANLIGNIPDSIKDLKSIQNFDVAINNLTGKIPESIGELKTVEQIELFQNKFSGELPNTFSGLVSLFRFDASQNNLTAKIPDSLARLPLVSLNLNDNNLEGEIPESLSLNPNLTQFKLFNNRFSGTLPQDFGLSSDLDEFDVSGNNLEGSLPPNLCSRYKLRILNLFDNRFSGSIPESYGECNSLTYVRIYNNQFSGELPTGFWSFVGYTFLELRNNNFQGSIPASISNARGLTEILISGNKFSGELPAGLCNFEEIVIMDISKNQLSGELPSCITKLKTLQKLDLSENRITGRIPKLISSWTDLTELNLANNQLTGEIPGELGTLPVLTYLDLAGNLLSGEIPTELSNLKLNKFNVSNNRLEGKVPLVFDNDFFISGLQGNPDLCSPDLKPLPQCPRPKSISLYLVCILSALAVILVGSLVWVLIKAKKLLPIQSKRKSAWRITAFQRVGFTEGDLLASLTNENLIGAGGSGRVYRVKLKSGQMVAVKKLWEAKRERESEEVFKSEVETLGTVRHGNIVKLLYSGIGEDFRILVYEYMENGSLGDVLHGEKGGILLDWPRRFGIAVGAAQGLAYLHHDSVPAIVHRDVKSNNILLDEDFRPKVADFGLAKVMQHDSEESDQVMSHIAGSYGYIAPEYAYTLKINEKSDVYSFGVVLLELITGKRPNDSSFGENTDMVKWVLEVAISSKKDEGSVRVMGSNSILDLKQLVDQRMNPSASNYAEIKKVFDVALLCTSSLPINRPSMRRVVELLKDNSVARSKSIR
Gene start	4601
Gene end	8400
Strand	1

Supplemental Data S3

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NbenIDA1A      ----------CCACAAGCTTCTGTCAATTTCTGAC------GTGGAAGAGTTTACTTTTT  44
NtabIDA1B      ------------------TCAGTTGACTTGCAAA---AGAAAAGAAAAAAAATACTATTT  39
NtomIDA1       ------------------TCAGTTGACTTGCAAA---AGAAAAGAAAAAAAATACTATTT  39
NbenIDA1B      GGGAAACTCATGAGAAAATCCCTTAAGTTG----------ACTTAAAAAAAACATTATT  49
NtabIDA1A      ------CTCATAAGAAAATCCCTTCAGTTGACTTGAAAAAGAAAAAGAAAAACATTATTT  54
NsylIDA1       -------TCATAAGAAAATCCCTTCAGTTGACTTGAAAAAGAAAAAGAAAAACATTATTT  53
                             *    * * **                 *  *      *  **

NbenIDA1A      -TCC-------AAATTTTAGCTGTTCTGGTCAAAGGGTTCTATACAGTATAATACCTAAA  96
NtabIDA1B      AAACAGGAAATAACTTTAGTCACCTCCGATCCGAT----CTTTACACCCAACTACATTAA  95
NtomIDA1       AAACAGGAAATAACTTTAGTCACCTCCGATCCGAT----CTTTACACCCAACTACATTAA  95
NbenIDA1B      CAACAGGAAATAACCTTAATCACTT-----CCGAT----ATTTATATCAAATTATATTAA 100
NtabIDA1A      CAACAGGAAATAACCTTAGCCACCT-----CAGAT----ATTTACACCAGATTATATTAA 105
NsylIDA1       CAACAGGAAATAACCTTAGCCACCT-----CAGAT----ATTTACACCAGATTATATTAA 104
                  *       **  **   *   *     *  *      * ** *    * **  * **

NbenIDA1A      CTTAAAGTAAGATTATTATCTAATTTTAGTAAAACTGGTTTGATTAAAATATTATTATGA 156
NtabIDA1B      TTTATCATAA-TTAATATTA-------TAAAAATATTGACAAATGTACTAACTAGCTATA 147
NtomIDA1       TTTATCATAA-TTAATATTA-------TAAAAATATTGACAAATGTACTAACTAGCTATA 147
NbenIDA1B      TTTATATTAG-TTA-ATATT-------AAAAAATATTGATAGATGTACGGACTAGCTATA 151
NtabIDA1A      TTTATATTAA-TTA-ATATT-------AAACAATATTGACAGATGTACTGACTAGCTATA 156
NsylIDA1       TTAATATTAA-TTA-ATATT-------AAAAAATATTGACAGATGTACTGACTAGCTATA 155
                * *   **   *     *           **  * *    **  *   * **     *

NbenIDA1A      ACGGGTAAACCTAAATTTATGCATAAAGATAA--------CTAAATAGTGTTCATTGGTT 208
NtabIDA1B      ATTCAGTGACAAAAGTTTATGCATAAAAATATTAATACATATATTAAGTATTCAAT-GGT 206
NtomIDA1       ATTCAGTGACAAAAGTTTATGCATAAAAATATTAATACATATATTAAGTATTCAAT-GGT 206
NbenIDA1B      ATTCAGTGACAAAAGTTTATGCATAAAAATAC------ATAAAGCAAATATTTATT-GGT 204
NtabIDA1A      ATTCAGTGACAAAAGTTTATGCATAAAAATAC------ATAAAGCAAGTATTTATT-GGT 209
NsylIDA1       ATTCAGTGACAAAAGTTTATGCATAAAAATAC------ATAAAGCAAGTATTTATT-GGT 208
               *       **  ** ************ ***          *   * * ** * * * *

NbenIDA1A      CGATGTAAATATCGTGTCAAATT-TTTTTCCTTAAAACATATACTCCATAAGAAGAAAAC 267
NtabIDA1B      TGATGTAAACATCGTGTATGTGTGTAAAATTTTTCCCCTTAAAACAGATAAGAAGAAAAC 266
NtomIDA1       TGATGTAAACATCGTGTATGTGTGTAAAATTTTTCCCCTTAAAACAGATAAGAAGAAAAC 266
NbenIDA1B      TGTTATAAATATCGTGTATGTGTGTAAAATTTTTCTCTT-AAAACATATAACAAGAAAAC 263
NtabIDA1A      TGGTACAAGCATCGTGTATGTGTGTAAATTTTTTCTCTT-AAAACATATAAGAAGAAAAC 268
NsylIDA1       TGGTACAAGCATCGTGTATGTGTGTAAATTTTTTCTCTT-AAAACATATAAGAAGAAAAC 267
                * *  **  *******     * *      **       * *    **** ********

NbenIDA1A      GCCGGCGTTTATTCCAAATCATTTAATATATATTTTTTCTTATCAGTTGACATTTATCAA 327
NtabIDA1B      GCCGGCATTTATTCCAAATCATT-TAATATAGTTTTTTCTTATCAGTTGACATTTATTAA 325
NtomIDA1       GCCGGCATTTATTCCAAATCATT-TAATATAGTTTTTTCTTATCAGTTGACATTTATTAA 325
NbenIDA1B      GCCGGCGTTTATTCCAAATCATTTA-ATAATTTTTTTTCTTATCAGTTGACATTTATTAA 322
NtabIDA1A      GCCGGCGTTTATTCCAAATCA-TTTAATATATTTTTTTCTTATCAGTTGACATTTATTAA 327
NsylIDA1       GCCGGCGTTTATTCCAAATCAATTTAATATATTTTTTTCTTATCAGTTGACATTTATTAA 327
               ****** ************** *         ************************** **
                                                          drought

NbenIDA1A      AGAATTGTTTAATTTAGTCGTTTGACGTGTGAATCACTTAACCTTTATTGCCGAACTCTT 387
NtabIDA1B      AGAATTGTTTAATACAGTCGTTTGACGTGTGAATCACTTAACCTTTTTTGCCGAACTCTT 385
NtomIDA1       AGAATTGTTTAATATAGTCGTTTGACGTGTGAATCACTTAACCTTTTTTGCCGAACTCTT 385
NbenIDA1B      AGAATTGTTTAATTTAGTCGTTTGACGTGTGAATCACTTAACCTTTTTCGCCGAACTCTT 382
NtabIDA1A      AGAATTGTTTAATTTAGTCGTTTGACGTGTGAATCACTTAACCTTTTTTGCCGAACTCTT 387
NsylIDA1       AGAATTGTTTAATTTAGTCGTTTGACGTGTGAATCACTTAACCTTTTTTGCCGAACTCTT 387
               *************  ******************************** * ***********
                                auxins
                                methyl jasmonate
                                abscisic acid

NbenIDA1A      TGCTTCCCCATGCACATACATTTGCACATATATATAAC-----CCTACTTCTTTTGCCTA 442
NtabIDA1B      TACTTCCCCATGCACATACATTTCCTCATATATATAT---AACCCTACTTCATTTACTTA 442
NtomIDA1       TACTTCCCCATGCACATACATTTCCTCATATATATAT---AACCCTACTTCATTTACTTA 442
NbenIDA1B      TACTTCCCCATGCACATATATTTGCTCATATATATAACCCAACCCTACTTCATTTACTTA 442
NtabIDA1A      TGCTTCCCCATGCACATACATTTGCACATATATATAACCC-----TACTTCATTTACTTA 442
NsylIDA1       TGCTTCCCCATGCACATACATTTGCACATATATATAACCC-----TACTTCATTTACTTA 442
               * ***************** **** * **********         ****** *** * **
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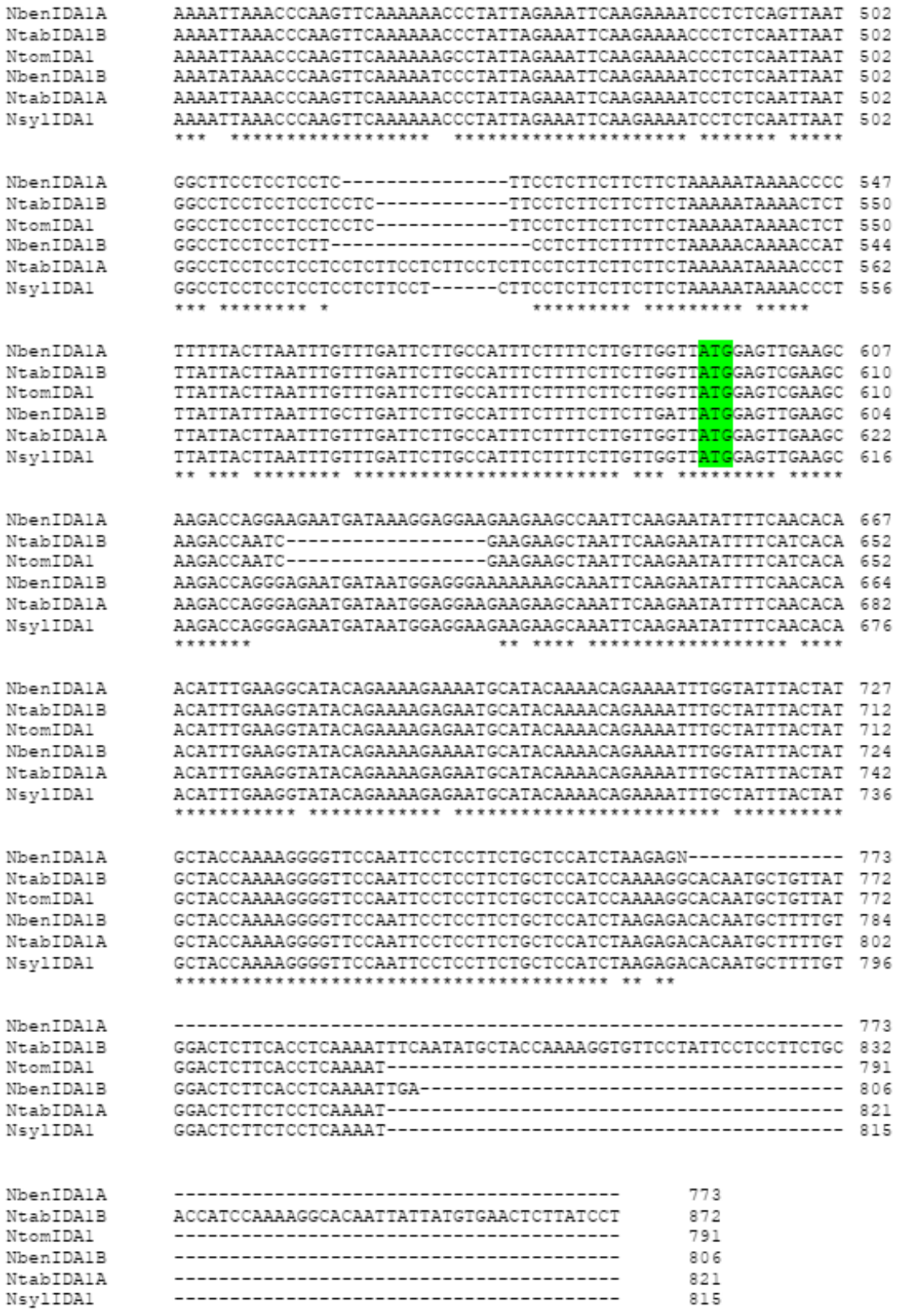

Alignment of the 5′-UTR sequences (500 bp) and the CDS of *NbenIDA1A*, *NbenIDA1B*, *NtabIDA1A*, *NtabIDA1B*, *NsylIDA1* and *NtomIDA1* genes. Start codon is highlighted in green, and *cis*-acting regulatory elements are highlighted as follows: brown line, abscisic acid; blue line, methyl jasmonate; red line, auxins; grey line, drought.