UNIVERSIDADE ESTADUAL DE CAMPINAS
INSTITUTO DE BIOLOGIA

NAÍRA COSTA SOARES BARBOSA

Efeitos dos hormônios vegetais citocinina e giberelina na transição de fases em *Passiflora* spp. (Passifloraceae)

Effects of cytokinin and gibberellin on phase change in *Passiflora* spp. (Passifloraceae)

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Tese apresentada ao Instituto de Biologia da Universidade Estadual de Campinas como parte dos requisitos exigidos para a obtenção do Título de Doutora em Biologia Vegetal

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Orientador: MARCELO CARNIER DORNELAS

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Os membros da Comissão Examinadora acima assinaram a Ata de Defesa, que se encontra no processo de vida acadêmica do aluno.

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RESUMO

As plantas possuem três principais fases no seu ciclo de vida: juvenil, adulta vegetativa e reprodutiva. A passagem para a fase reprodutiva, quando ocorre o florescimento, tem sido muito estudada. Contudo, a transição da fase juvenil para a adulta vegetativa necessita de melhor compreensão, principalmente em nível molecular. Grande parte dos estudos de transições de fases realizados foram com a espécie modelo *Arabidopsis thaliana*, mas há necessidade de entender como estes processos ocorrem em outras espécies. As espécies do gênero *Passiflora* são ótimos modelos para estudos de desenvolvimento vegetal, pois há diferenças morfológicas evidentes entre as plantas nas fases juvenil, adulta vegetativa e adulta reprodutiva. Em *Passiflora* não há gavinhas na fase juvenil. Na fase adulta vegetativa, surgem gavinhas a partir de meristemas axilares das folhas e, na fase reprodutiva, surgem simultaneamente flores e gavinhas nas axilas das folhas. Sabe-se que os fitormônios influenciam diretamente o desenvolvimento vegetal, sobretudo as citocininas e as giberelinas. No presente estudo tivemos como objetivos: a) avaliar a influência da aplicação exógena de citocinina e giberelina em *P. organensis* durante a transição da fase juvenil para a fase adulta vegetativa; b) identificar e caracterizar possíveis ortólogos de genes envolvidos no metabolismo, sinalização e resposta a citocininas e giberelinas em *Passiflora*; e c) caracterizar o padrão de expressão dos genes relacionados a giberelinas. A aplicação de citocinina reprimiu o desenvolvimento das gavinhas, estimulou o desenvolvimento de ramos vegetativos a partir dos meristemas axilares, além de causar alterações morfológicas nas folhas, como desenvolvimento de lobos e deformidades, quando em doses mais altas. Por outro lado, a aplicação de giberelina estimulou o desenvolvimento precoce de gavinhas, crescimento acelerado das plantas e alterações morfológicas das folhas que apresentaram características adultas precocemente. Foram caracterizados os genes relacionados a síntese, degradação e resposta a citocininas e giberelinas. A maior parte dos ortólogos de *P. organensis* apresentou grande similaridade das sequências com outras espécies, sugerindo similaridade funcional. Analisamos a expressão de genes relacionados a síntese, catabolismo e resposta a giberelinas em plantas de *P. edulis* submetidas a aplicações de giberelina exógena, GA_3, e também em plantas submetidas a aplicações de paclobutrazol. As expressões dos genes tiveram alterações no sentido de balancear as concentrações da giberelina nas plantas, conforme relatado na literatura. Os

resultados obtidos poderão ser aplicados para futuros estudos de melhoramento genético tanto em espécies do gênero *Passiflora* com interesse comercial, como em outras espécies.

ABSTRACT

Plants have three main phases in their life cycle: juvenile, adult vegetative and reproductive. The transition to the reproductive stage, when flowering occurs, has been widely studied in model species. However, the transition from the juvenile to the adult vegetative stages needs to be better understood, especially at the molecular level. Most of the phase transition studies in the literature were performed with the model species *Arabidopsis thaliana*, but there is a need to understand how these processes occur in other species. The species of the genus *Passiflora* are excellent models for studies of plant development, as there are evident morphological differences between plants in the juvenile, vegetative adult and reproductive stages. In *Passiflora* there are no tendrils in the juvenile stage. In the vegetative adult stage, tendrils appear from the leaf axillary meristems, and in the reproductive stage, flowers appear simultaneous to tendrils, in the leaf axils. It is known that phytohormones directly influence plant development, especially cytokinins and gibberellins. In the present study we had as goals: a) to evaluate the influence of the exogenous application of cytokinin and gibberellin in *P. organensis* during the transition from the juvenile to the vegetative adult phase; b) identify and characterize possible orthologs of genes involved in metabolism, signaling and response to cytokinins and gibberellins in *Passiflora*; and c) characterize the expression pattern of genes related to gibberellins. The application of cytokinin repressed the development of tendrils, stimulated the development of vegetative branches from the axillary meristems, in addition to causing morphological changes in the leaves, such as the development of lobes and deformities, when at higher doses. On the other hand, the application of gibberellin stimulated the early development of tendrils, accelerated plant growth and morphological changes in leaves that showed early adult characteristics. Genes related to synthesis, degradation and response to cytokinins and gibberellins were characterized. Most of the *P. organensis* orthologs showed great sequence similarity with other species, suggesting functional similarity. We analyzed the expression of genes related to synthesis, catabolism and response to gibberellins in *P. edulis* plants submitted to exogenous gibberellin, GA_3, and also in plants submitted to paclobutrazol applications. Gene expressions changed in order to balance gibberellin concentrations in plants, as reported in the literature. The results obtained can be applied to future studies of genetic breedingh both in species of the genus *Passiflora* with commercial interest, as in other species.

SUMÁRIO

INTRODUÇÃO GERAL

Estudos de transição de fases em vegetais possuem grande importância científica e econômica, pois o desenvolvimento de flores e posteriormente de frutos depende da mudança da fase vegetativa para a fase reprodutiva. Do ponto de vista comercial, entender os fatores que afetam o tempo e a duração da fase juvenil é de grande utilidade para o planejamento de colheitas, como no desenvolvimento de métodos para diminuir ou aumentar o tempo de florescimento, ou para prolongar o estágio vegetativo (Matsoukas et al. 2014; Lawrence et al. 2021a). Portanto, a compreensão de como a mudança da fase vegetativa é regulada fornece uma base para a manipulação de características de interesse agronômico.

O ciclo de vida das plantas é dividido em três fases distintas em seu desenvolvimento pós-embrionário: juvenil, adulta vegetativa e adulta reprodutiva (Poethig 1990). O que diferencia cada fase são os órgãos formados a partir do meristema caulinar ao longo do ciclo de vida da planta. O meristema vegetativo forma novas folhas, enquanto o meristema floral produz flores que formam sementes após a fertilização (Bartrina et al. 2011). Antes de se tornarem competentes para florescer e se reproduzir, as plantas passam por um período de crescimento vegetativo, subdividido em fase juvenil e fase adulta vegetativa (Huijser e Schmid 2011). Esta transição nem sempre implica em alterações morfológicas evidentes, embora as alterações moleculares observadas possuam um padrão de desenvolvimento que se aplica aos vegetais em geral (Poethig 1990). Quando presentes, as alterações morfológicas mais visíveis entre a fase juvenil e a adulta vegetativa são mudanças na morfologia foliar, que permitem que se observem ramos juvenis e adultos na mesma planta (Yang et al. 2013; Manuela e Xu 2020). Posteriormente, na transição da fase adulta vegetativa para a adulta reprodutiva, o meristema apical caulinar vegetativo torna-se um meristema de inflorescência e há produção de meristemas florais (Huijser e Schmid 2011).

A transição da fase adulta vegetativa para a reprodutiva tem sido analisada em diversas espécies, tanto sob nível morfológico como molecular, buscando compreender os mecanismos que levam ao surgimento de flores e posterior desenvolvimento de frutos (Nilsson et al. 1998; Giacomelli et al. 2013; Jung et al. 2014). Por outro lado, a transição da fase juvenil para a adulta vegetativa foi menos estudada, embora mais recentemente estejam sendo realizados estudos para buscar compreendê-la (Poethig 2010; Ahsan et al. 2019; Manuela e Xu 2020; Lawrence et al. 2021b; Gioppato e Dornelas 2021), considerando a importância desta transição para a definição da estrutura da planta.

Análises moleculares em diferentes espécies permitiram a identificação de diversos genes que participam da regulação das transições de fases em vegetais (Amasino e Michaels 2010; Mouradov et al. 2002; Srikanth e Schmid 2011). Na transição juvenil para adulta vegetativa, o controle genético é basicamente realizado por dois micro RNAs, miR156 e miR172 seus genes alvos, SPLs (Wang e Wang 2015; Ahsan et al. 2019; Manuela e Xu 2020; Gioppato e Dornelas 2021). A transição da fase juvenil para a adulta vegetativa está associada a uma queda nos níveis de miR156 e um aumento nos de miR172 nas folhas (Ahsan et al. 2019; Manuela e Xu 2020).

Há diversas vias metabólicas e de sinalização dos genes relacionados às transições que são influenciadas por fatores ambientais, como fotoperíodo e temperatura, e endógenos, como concentração de fitormônios e açúcares (Amasino e Michaels 2010; Mouradov et al. 2002; Srikanth e Schmid 2011). Dentre estes fatores, a concentração dos fitormônios possui papel de destaque que vem sendo estudado em várias espécies (Evans e Poethig 1995; Crane et al. 2012; Tenreira et al. 2017; Giacomelli et al. 2013; Cheng et al. 2021). As giberelinas (GAs) podem apresentar papéis antagônicos na transição para a fase reprodutiva, induzindo o florescimento em diversas espécies, como *Arabidopsis thaliana* (Blázquez et al. 1998; Bao et al. 2020), rabanete (*Raphanus sativus* L.) (Jung et al. 2020) e crisântemo (*Chrysanthemum morifolium*) (Dong et al. 2017) e reprimindo em várias outras como maracujá (*Passiflora edulis*) (Nave et al. 2010), pinhão manso (*Jatropha curcas* L.) (Li et al. 2018), e árvores frutíferas tais como manga (*Mangifera indica* L.) (Nakagawa et al. 2012), maçã *(Malus domestica*) (Zhang et al. 2019) e laranja (*Citrus sinensis*) (Lord e Eckard 1987; Goldberg-Moeller et al. 2013). Em *Zea mays*, observou-se que GAs promoveram tanto a passagem da fase juvenil para a adulta vegetativa, como também para a fase adulta reprodutiva (Evans e Poethig 1995). As citocininas (CKs) também estão relacionadas à regulação dos meristemas e à indução do florescimento (Krajnčič 1983; Eshghi e Tafazoli 2007; D’Aloia et al. 2011). Foi demonstrado que esta classe de fitormônios regula o tamanho e a atividade dos meristemas de inflorescência em *A. thaliana* (Bartrina et al. 2011), através da ativação de genes relacionados, como *TWIN*

SISTER OF FT (*TSF*) e *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1* (*SOC1*) (D'Aloia et al. 2011).

Ambos os fitormônios, GAs e CKs, atuam na decisão sobre o destino dos meristemas (Crane et al. 2012; Sobol et al. 2014; Tenreira et al. 2017). Contudo, podem atuar de maneira oposta. Este comportamento foi observado em *Passiflora edulis*, cujo gênero é objeto de estudo do presente trabalho, na qual o florescimento foi inibido pela aplicação de GA_3 (Sobol et al. 2014), mas estimulado pela aplicação de CK (Cutri et al. 2013).

Arabidopsis thaliana tem sido muito utilizada como modelo em estudos de desenvolvimento (Okada 1991; D'Aloia et al. 2011). Contudo, há necessidade de se utilizar outras espécies modelos para estudos de transição de fases, que tenham, por exemplo, outras estruturas como as gavinhas, que não estão presentes em *A. thaliana*, e assim se possa ter uma compreensão mais clara de como esse processo ocorre nos vegetais em geral. As plantas da família Passifloraceae, conhecidas popularmente como maracujás, são consideradas excelentes modelos para estudos de desenvolvimento, pois algumas delas apresentam uma clara diferenciação morfológica entre as três fases do desenvolvimento (Nave et al. 2010; Cutri et al. 2013; Fernandes et al. 2020). A família possui cerca de 932 espécies e 36 gêneros (The Plant List 2020) com distribuição pantropical (Souza e Lorenzi 2012).

Pertencente à ordem Malpighiales (APG III 2009), Passifloraceae inclui trepadeiras ou lianas com gavinhas axilares (Judd et al. 2009). O monofiletismo do grupo é bem sustentado pela presença de uma corona bem desenvolvida nas flores (Brizicky 1961) e por caracteres moleculares (Muschner et al. 2003; Judd et al. 2009; Tokuoka 2012). No Brasil, há cerca de 166 espécies de Passifloraceae aceitas, sendo 90 endêmicas (Bernacci et al. 2020). São plantas com caule lenhoso e lignificado na base, porém herbáceo e pouco lignificado no ápice (Kluge 1998). As folhas apresentam grande diversidade morfológica, podendo ser simples, lobadas ou digitadas, com bordos lisos ou serreados, alternas e espiraladas, e, em geral, há nectários no pecíolo (Kluge 1998; Judd et al. 2009). As flores são hermafroditas, diclamídeas e axilares (Kluge 1998; Judd et al. 2009). O cálice e a corola são pentâmeros, geralmente apresentam cinco estames, dispostos em um pedúnculo junto com o gineceu, constituindo o androginóforo que com a corona são as características mais marcantes da família (Judd et al. 2009).

Há duas tribos dentro de Passifloraceae: Paropsieae e Passifloreae, sendo que apenas a segunda ocorre no Brasil (Wilde 1971; 1974; Escobar 1988). Os quatro gêneros que ocorrem no Brasil são: *Ancistrothyrsus* Harms, *Dilkea* Mast., *Mitostemma* Mast. e *Passiflora* L. (Wilde 1971; Bernacci et al. 2020). O gênero *Passiflora* é o mais numeroso, com cerca de 560 espécies (Krosnick et al. 2013), sendo a maioria originária da América Tropical (Oliveira e Ruggieiro 2005). Este possui cinco subgêneros: *Astrophea*, *Decaloba*, *Passiflora*, *Deidamioides* (Wilde 1974; Cervi 2006) e *Tetrapathea* (Krosnick et al. 2009).

Os dois subgêneros mais diversificados são *Passiflora* e *Decaloba* com 250 e 230 espécies, respectivamente (Porter-Utley 2014). O subgênero *Passiflora* contém as espécies de maior interesse econômico, sendo utilizadas na alimentação, como *P. edulis* (maracujá-amarelo) (Meletti e Maia 1999) e *P. alata* (maracujá doce) (Alves et al. 2012) e na indústria farmacêutica, como *P. alata* (Figueiredo et al. 2016) e *P. incarnata* (Miroddi et al. 2013). Este subgênero inclui trepadeiras herbáceas e lianas, com flores grandes e coloridas (Ulmer e MacDougal 2004). O subgênero *Decaloba*, por sua vez, contém pequenas trepadeiras e arbustos (Ulmer e MacDougal 2004), com inflorescências paucifloras, flores frequentemente pequenas, brancas ou amareladas e corona com uma ou duas séries de filamentos (Milward-de-Azevedo e Baumgratz 2004).

Uma das espécies escolhidas como modelo para o presente trabalho foi *Passiflora organensis*, subgênero *Decaloba*, por ter o genoma totalmente sequenciado pelo nosso grupo de pesquisa (Costa et al. *in press*) e apresentar uma clara diferenciação entre as três fases do desenvolvimento. O epíteto específico *organensis*, referese ao local de coleta do exemplar-tipo, na Serra dos Órgãos, município de Teresópolis, Rio de Janeiro (Milward-de-Azevedo e Baumgratz 2004). *P. organensis* está distribuída geograficamente nas Regiões Sudeste e Sul do Brasil, geralmente em Floresta Ombrófila Densa (Mondin et al. 2011), ocorrendo nos estados de Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina e Rio Grande do Sul (Milward-de-Azevedo e Baumgratz 2004). O florescimento ocorre nos meses de verão (Mondin et al. 2011).

As espécies do gênero *Passiflora*, em geral, não apresentam gavinhas na fase juvenil (Cutri et al. 2013). O surgimento das gavinhas a partir dos meristemas presentes nas axilas das folhas marca o início da fase adulta vegetativa (Nave et al. 2010; Cutri et al. 2013). Posteriomente, os mesmos meristemas formam adicionalmente, uma ou mais flores (Krosnick e Freudenstein 2005; Nave et al. 2010; Cutri et al. 2013). Desta forma, quando os botões florais se desenvolvem, estes são formados lado a lado com as gavinhas (Ulmer e MacDougal 2004; Nave et al. 2010; Cutri et al. 2013).

Essa plasticidade ontogênica do meristema axilar, que pode originar estruturas distintas, pode ser modulada por fatores ambientais como fotoperíodo e temperatura, ou endógenos, como concentração de fitormônios (Cutri et al. 2013). Compreender como funcionam os mecanismos moleculares que regulam as transições de fases possibilita a sua manipulação, havendo diversas implicações científicas e na produção vegetal (Matsoukas et al. 2014).

Em algumas espécies do gênero, além do surgimento de gavinhas e flores, com a mudança de fases ocorrem também alterações morfológicas nas folhas (Chitwood e Otoni 2017). Em *P. edulis,* por exemplo, as folhas juvenis são lanceoladas, enquanto as folhas da fase adulta são trilobadas (Figura 1) (Ulmer e MacDougal 2004; Fernandes et al. 2020).

Figura 1. Diferenças morfológicas em *Passiflora edulis* nas diferentes fases do desenvolvimento. A. Folha juvenil lanceolada. B. Folha adulta trilobada. Barra: 1cm. Fotos: Naíra C. S. Barbosa.

Na espécie utilizada no presente estudo, *P. organensis*, quando a planta passa para a fase adulta vegetativa, surge uma gavinha a partir de um meristema axilar da folha, e na passagem para a fase adulta reprodutiva, surgem duas flores além da gavinha (Figura 2).

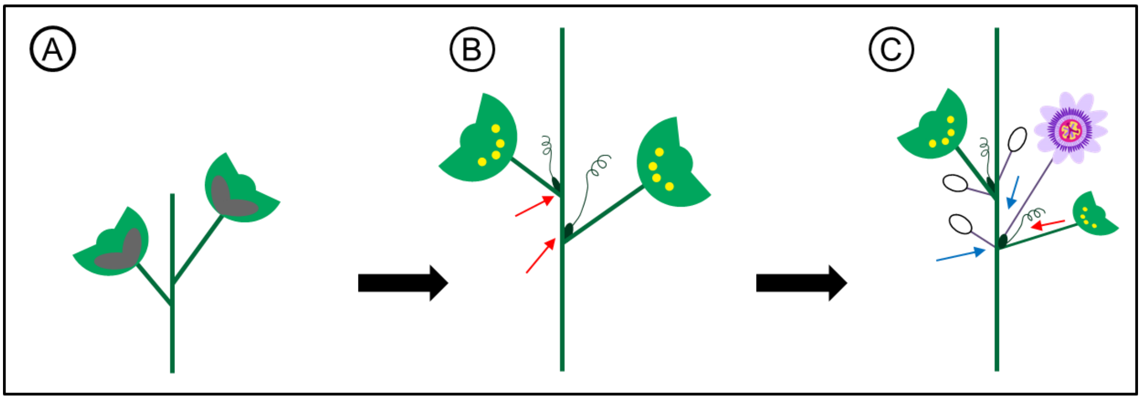

Figura 2. Diferenças morfológicas em *Passiflora organensis* nas diferentes fases do desenvolvimento. A. Fase juvenil – folhas com manchas acinzentadas na face adaxial. B. Fase adulta vegetativa – folhas sem as manchas acinzentadas e com nectários extraflorais (discos amarelos), gavinhas a partir de meristemas axilares (setas vermelhas). C. Fase adulta reprodutiva – além das gavinhas (setas vermelhas), surgem duas flores a partir de meristemas axilares (setas azuis).

As folhas de *P. organensis* apresentam durante a fase juvenil uma mancha de coloração acinzentada, e na fase adulta perdem essa mancha e surgem nectários extraflorais na face adaxial (Figura 3) (Ulmer e MacDougal 2004; Brasileiro 2014; Chitwood e Otoni 2017). Além disso, suas folhas possuem grande plasticidade morfológica, podendo variar de acordo com o ambiente e, por isso podem ser confundidos com outras espécies como *P. misera* e *P. pohlii* (Milward-de-Azevedo e Baumgratz 2004).

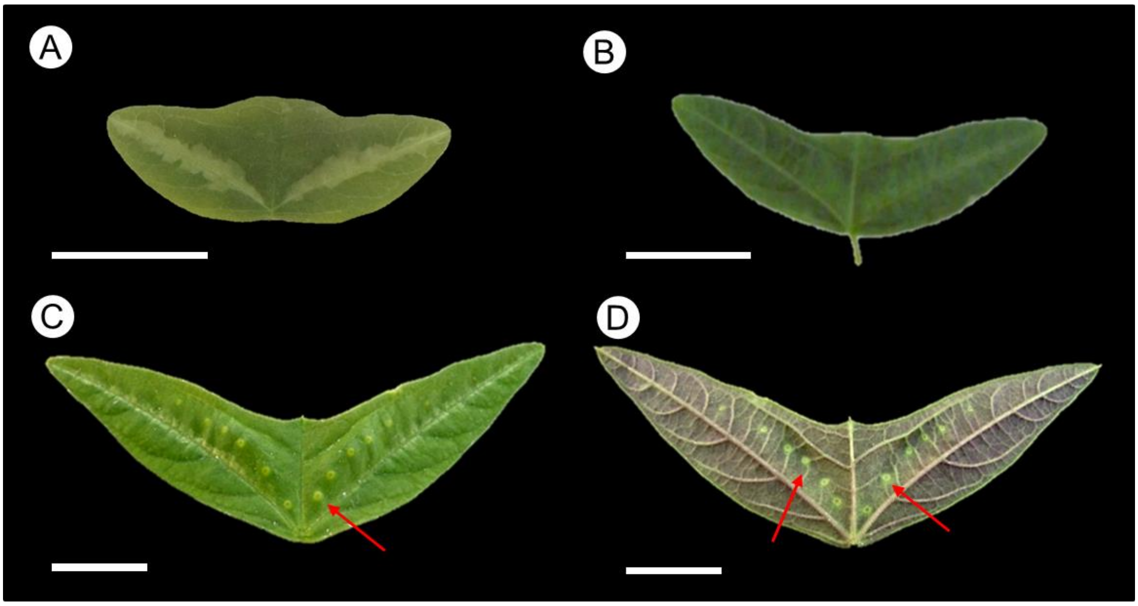

Figura 3. Diferenças morfológicas em *Passiflora organensis* nas diferentes fases do desenvolvimento. A. Folha juvenil face adaxial evidenciado as manchas acinzentadas. B. Folha juvenil face abaxial. C. Folha adulta face adaxial sem as manchas acinzentadas e com os nectários extraflorais (setas vermelhas). D. Folha adulta face abaxial com os nectários extraflorais (setas vermelhas). Barra: 1cm. Fotos: Naíra C. S. Barbosa.

Com este estudo, buscamos compreender como os fitormônios citocinina e giberelina regulam a transição da fase juvenil para a adulta vegetativa, utilizando como modelo a espécie *P. organensis*. O presente trabalho foi dividido em quatro capítulos. O Capítulo I é um artigo de revisão já publicado (Barbosa e Dornelas 2021) no qual resumimos como CKs e GAs atuam durante as transições de fase em plantas modelo e em algumas espécies tropicais, sobretudo em *Passiflora* spp., analisando seus mecanismos moleculares de ação e as vias metabólicas nas quais interferem. No Capítulo II, analisamos as alterações morfológicas na transição juvenil para adulta vegetativa causadas por aplicações de CKs e GAs em *Passiflora organensis*. Para analisar como a concentração destes fitormônios influencia a expressão dos genes relacionados ao seu controle em *Passiflora* spp., identificamos e caracterizamos, no Capítulo III, os ortólogos dos principais genes relacionados à biossíntese, ao catabolismo, à sinalização e à resposta a CKs e GAs em *P. organensis*. E por fim, no Capítulo IV, analisamos o padrão de expressão de alguns destes ortólogos identificados, em plantas de *P. edulis* submetidas a aplicações de GAs, para compreender a interação entre aplicações exógenas e a regulação dos genes de metabolismo e resposta de giberelinas.

Estas informações ajudarão a elucidar a transição de fases juvenil-adulto vegetativo em vegetais, que ainda é pouco compreendida. Além disso, podem ser de grande utilidade para estudos futuros de melhoramento da produção de espécies de maracujazeiro com interesse comercial, e de outras espécies tropicais cultivadas.

OBJETIVOS

Diante do exposto, nos propomos a responder à seguinte pergunta:

Como as citocininas e giberelinas influenciam na transição da fase juvenil para a adulta vegetativa em espécies de *Passiflora* nos níveis morfológico e molecular?

Objetivos específicos:

- Analisar os efeitos dos fitormônios citocinina e giberelina nas transições de fases em vegetais em geral, focando nas interações moleculares entre estas classes de fitormônios.
- Avaliar a influência das aplicações de citocinina e giberelina na morfologia de plantas de *P. organensis* durante a transição de fase juvenil para adulta vegetativa.
- Identificar os ortólogos de genes responsáveis pelo controle hormonal (de citocininas e giberelinas) no genoma de *P. organensis*.
- Observar os efeitos de diferentes concentrações de giberelina exógena na expressão dos genes candidatos identificados - relacionados ao metabolismo e resposta a giberelinas - em plantas de *P. edulis*.

CAPÍTULO I - The roles of gibberellins and cytokinins in plant phase transitions

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Abstract

Plants undergo distinct phase transitions during their postembryonic development and progresses from the juvenile to the adult and reproductive phases. These transitions are characterized by morphological and molecular changes and are differently influenced by gibberellins (GAs) and cytokinins (CKs). GAs are notably known to either induce or repress phase transition and flowering in diverse plant species. This GA mediated modulation is ultimately related to the behavior of the DELLA transcriptional regulators. CKs influence phase transitions by promoting meristem cell divisions and flowering stimulation. Moreover, CKs and GAs can mutually repress each other or have complementary functions in processes such as branching and flowering. Therefore, the effects observed such as flower formation and vegetative growth is modulated by the coregulation exerted by the crosstalk of both GA and CK pathways. We review the roles of GA and CK in phase transitions at the molecular level in model species such as *Arabidopsis* and the genes that are modulated by both GA and CK pathways. Additionally we point out perspectives of the conservation of these molecular pathways in tropical plants.

Keywords: Cytokinin, gibberellin, phase change, phytohormones, plant development.

Introduction

Plant phase transitions are characterized by morphological (Araki 2001; Matsoukas 2014) and molecular changes (Mouradov et al. 2002; Voogd et al. 2017), which are triggered and regulated by both environmental stimuli (photoperiod and temperature) and endogenous stimuli (phytohor mones and carbohydrate concentration) (Amasino and Michaels 2010; Srikanth and Schmid 2011). Since phytohormones play a leading role in all stages of plant development, their individual effects and interactions have been studied in several species (Evans and Poethig 1995; Crane et al. 2012; Tenreira et al. 2017). This paper focuses on the roles of two classes of phytohormones in phase transitions: gibberellins (GAs) and cytokinins (CKs).

GAs are notably known to have opposite effects on flower transition in different species (De Dios et al. 2019). They are considered to either induce flowering in some, such as *Arabidopsis thaliana*, *Malus domestica* and *Brassica oleracea* (Looney et al. 1985; Blázquez et al. 1998; Mutasa-Göttgens and Hedden 2009; Duclos and Björkman 2015) or repressing flowering in others, such as Prunus persica and many tropical perenials such as Eucalypthus, *Passiflora edulis*, *Persea amaericana*, *Mangifera indica* and *Jatropha curcas* (Griffin et al. 1993; Salazar-Garcia and Lovatt 2000; Davenport 2007; An et al. 2008; Li et al. 2018). CKs also regulate the activity of meristem and might induce flowering in many species (Krajnčič 1983; Eshghi and Tafazoli 2007; D'Aloia et al. 2011). This class of phytohormones has been shown to regulate the size and activity of inflorescence meristems in *Arabidopsis* (Bartrina et al. 2011; D'Aloia et al. 2011).

In this review we summarize how GAs and CKs act on model plants during phase transitions by analyzing their molecular mechanisms of action and the metabolic pathways with which they interfere. We will focus on some case studies about the role of GAs and CKs in phase transitions and flowering of subtropical and trop ical fruit perennial species such as passion fruit (*Passiflora edulis*). Finally, we present perspectives for the molecular conservation of phase transition pathways in tropical and subtropical perennial species and the potential application of this knowledge in improving yield and plant breeding.

Morphological markers of plant phase transitions and particularities of some tropical and subtropical plants

After germination, and before becoming competent to flower, the plants undergo a period of vegetative growth, subdivided into the juvenile phase and adult vegetative phase (Huijser and Schmid 2011). In the juvenile to adult transition, not all species show visible morphological changes. In some model species, these changes are generally related to subtle modifications of morphology of leaves and stems (Fig. 1a). For example, there is loss of leaf epicuticular wax in Zea mays and the presence of trichomes differentiated on both leaf surfaces in *Arabidopsis thaliana* (Evans and Poethig 1995; Telfer et al. 1997; Poethig 2013). Nonetheless, a significant number of tropical species, especially perennial ones, show a quite abrupt demarcation between juvenile and adult vegetative phases and therefore are called "heteroblastic" species (Zotz et al. 2011). Thus, although some authors could consider *Arabidopsis* to be slightly heteroblastic (Poethig 2013), tropical species such as passion fruit (*Passiflora edulis*) are remarkably heteroblastic (see Fig. 1b), as juvenile plants are tendrilless and differentiate lanceolate leaves, while adult vegetative plants have tendrils in the axils of trilobed leaves.

One might argue that *A. thaliana* is an herbaceous annual species while *Passiflora* species are generally perennial ones. But there seems to have no correlation between heteroblasty and a given species being perennial or annual (Ahsan et al. 2019; Jameson and Clemens 2019). Although some tropical tree species such as *Eucalyptus* show readily recognizable different morphologies between juvenile and adult leaves (Griffin et al. 1993), a great number of tropical species, especially perennial fruit trees such as macadamia (*Macadamia integrifolia*), avocado (*Persea americana*) and mango (*Mangifera indica*) show no remarkable morphological differences between juvenile and adult plants (Ahsan et al. 2019). These are considered "homoblastic" species (Zotz et al. 2011; Jameson and Clemens 2019). In these cases the only morphological marker available to distinguish a juvenile plant from a reproductive one is the presence of floral buds on the plant at the reproductive phase.

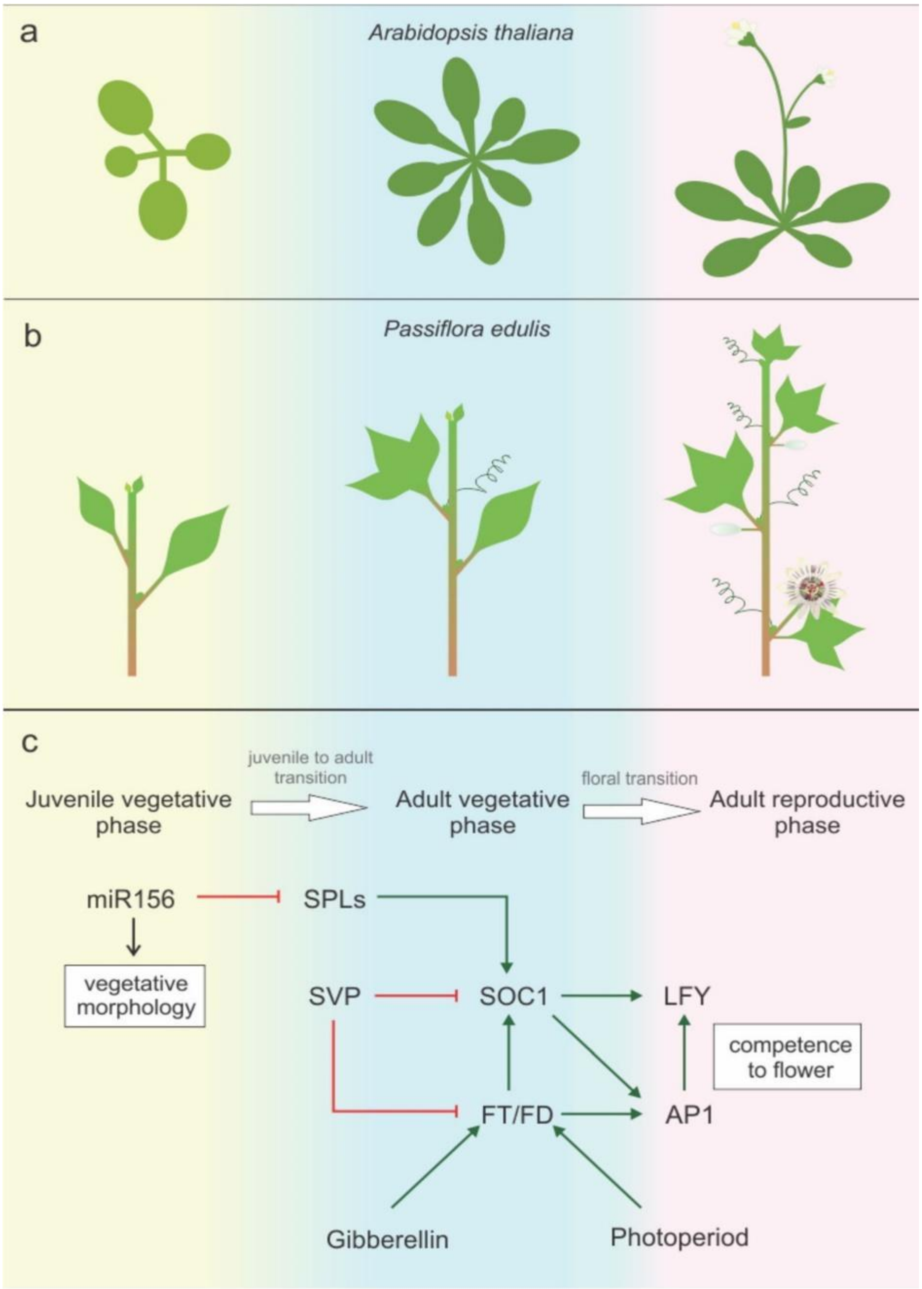

Figure 1. Plant phase transitions. (a) Key genes, main influential factors and interactions involved in juvenile to adult and floral transition in the model plant *Arabidopsis* thaliana (Adapted from Poethig 2013, Kaufmann et al. 2010). (b) Schematic repre sentations of juvenile, adult and reproductive plants of *A. thaliana*. (c) Schematic representations of juvenile, adult and reproductive plants of the tropical plant *Passiflora edulis*.(adapted from Cutri et al. 2013). In a, b and c the background color reflects the ju venile (yellow), adult (blue) or reproductive (pink) stages. AP1: APETALA1; FT/FD: FLOWERING LOCUS T and FLOWERING LOCUS D; LFY: LEAFY; miR156: microRNA 156; SOC1: SUPPRESSOR OF OVEREXPRESSION OF CONSTANS; SPLs: SQUAMOSA PROMOTER BINDING PROTEINLIKEs; SVP: SHORT VEGETATIVE PHASE

After the plant has ended the juvenile stage and transitioned to the adult phase, the vegetativetoreproductive transition is carried out in three steps in *Arabidopsis*: floral induction, ini tiation of flower, and floral development (Huijser and Schmid 2011;

Duclos and Björkman 2015; Wagner 2016). The first step is related to the fact that the apical shoot meristem no longer differentiates leaves, but (after perceiving inductive clues) promotes growth of the main shoot upwards and elongating shoot branches forming from the axils of the cauline leaves (Wagner 2016). The second step is related to the differentiation of floral meristems by the inflorescence meristem and the third step covers the development of floral organs until anthesis (Hyun et al. 2016; Wagner 2016). The conversion of the apical vegetative meristem into an indeterminate, raceme like inflorescence in *Arabidopsis* establishes a quite simple architecture (Fig. 1a). However, in many nonmodel subtropical and tropical species, especially perennial ones, the complexity of the behavior of axillary meristems blurs any attempt to compare phase transition processes with model plants such as *Arabidopsis*: After the transition to the reproductive stage, strawberry plants (*Fragaria vesca*) still can produce either vegetative (runners) or reproductive (inflorescences) structures from axillary meristems (Martins et al. 2018). Similarly, after entering the reproductive phase, axillary meristems of grape vines (*Vitis vinifera*) might produce either inflorescences or vegetative structures (tendrils), and in both species the proportion of nodes producing either vegetative or reproductive structures may vary according to environmental cues (Crane et al. 2012; Tenreira et al. 2017; Martins et al. 2018). It has been suggested that in grapevine the tendrils are modified flowers, as they already express genes that are considered to be markers of floral meristem identity in *Arabidopsis* (Calonje et al. 2004; Carmona et al. 2008). On the other hand, it is even more difficult to analyze reproductive development in passion fruit species (*Passiflora* spp.) as tendrils and inflorescences are produced simultaneously from the same axillary meristem (Cutri et al. 2013; Scorza et al. 2017, se also Fig. 1b). The tendrils of passion fruit plants are also considered to be modified portions of an inflorescence, and under special environmental conditions it is even possible to convert tendrils into additional shoots or flowers (Cutri et al. 2013).

It is thus clear that although model plants such as *Arabidopsis* are quite useful to understand the basics of the molecular pathways underlying phase transition, the complexity and morphological diversity of phase change markers in tropical fruit crops will impose much additional research efforts.

Key molecular aspects of phase transition in *Arabidopsis*

In *Arabidopsis*, phase transition is regulated by photoperiod (Simon et al. 1996), gibberellin (Blázquez et al. 1998), vernalization (Lee and Amasino 1995), plant age and sugars (Srikanth and Schmid 2011; De Dios et al. 2019). All these pathways converge on a few key genes that control the timing of flowering (Tan and Swain 2006, see also Fig. 1c). While *Arabidopsis* plants are in the juvenile phase, high levels of *miR156* prevents the accumulation of its targets, the members of the SQUAMOSA BINDING PROTEIN LIKE (SPL) family of transcription factors (Wu et al. 2009; Wang et al. 2011; Wagner 2016; Hyun et al. 2016). As SPLs promote flowering, high levels of miR156 keep *Arabidopsis* plants at the juvenile stage (Wu et al. 2009; Wang et al. 2011). As *Arabidopsis* progresses through the adult stage, levels of *miR156* drop drastically and SPL proteins begin to accumulate and directly activate the transcription of another microRNA, *miR172* (Wagner 2016; Hyun et al. 2016), which in turn represses the accumulation of six different *APETALA2*-like genes (Wu et al. 2009; Wang et al. 2011; Conti 2017). Some other genes may act more specifically into vernalization or autonomous pathways such as the transcription factors of the MADS-BOX family, *FLOWERING LOCUS C* (*FLC*) and *SHORT VEGETATIVE PHASE* (*SVP*) (Andrés et al. 2014, Mateos et al. 2015). This transcriptional modulation mediated by the miR156/miR172 balance affects the expression of floral inte grator genes such as *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS* (*SOC1*), *FLOWERING LOCUS T* (*FT*) and *FLOWERING LOCUS D* (*FLD*) (Kim et al. 2009; Bernier 2013; Andrés et al. 2014). These, in their turn, through con trolling the transcription of floral meristem identity genes, such as *APETALA1* (*AP1*), *FRUITFUL* (*FUL*), *TERMINAL FLOWER1* (*TFL1*) and *LEAFY* (*LFY*) regulate the formation of an inflorescence meristem and subsequently, floral meri stems (Simon et al. 1996; Wagner 2016).

Molecular aspects of the influence of GAs in phase transitions

GAs are a family of tetracyclic and diterpenoid plant hor mones (Hirano et al. 2008). They influence plant growth and development, such as seed germination, stem growth, floral organ development, pollen development, and fruit growth (Olszewski et al. 2002; Ogawa et al. 2003; Mutasa-Göttgens and Hedden 2009). Over 100 naturally occurring gibberellin molecules were identified, although only four are bioactiv ities:

GA_1, GA_3, GA_4 and GA_7 (Yamaguchi 2008). The bio synthesis of GAs takes place in three stages: entkaurene bio synthesis in chloroplasts, conversion of entkaurene in GA_{12} in the endoplasmic reticulum, and active gibberellins forma tion in the cytoplasm (Olszewski et al. 2002). The biosynthe sis of bioactive GAs involves the action of six enzymes and GA20OXIDASES (GA20OX) and GA3OXIDASESs catalyze the last step of activation, while the deactivation is cata lyzed by GA2OXIDASES (GA2OX) (Martins et al. 2018). Genes involved in GA metabolism show a differential pattern of expression among shoot apical meristem (SAM) tissues in different stages of development (De Dios et al. 2019).

The molecular mechanism of gibberellin action involves receptors encoded by the genes of the *GID1* family (Ueguchi-Tanaka et al. 2007) and transcriptional regulators of the DELLA family (Murase et al. 2008; Briones-Moreno et al. 2017). When the levels of GA increase, GA molecules are more likely to bind to GID1. Consequently, this complex GAGID1, interacts with the $SCF^{GID2/SLY}$ polyubiquitination complex, resulting in the degradation of DELLA proteins by the 26S proteasome (Murase et al. 2008) and therefore chang ing the trancriptional status of target genes (Nakajima et al. 2006). Additionally, DELLA proteins can be post traductionally modified, which interferes with their ability to directly or indirectly interact with different transcriptional regulators (Park et al. 2013).

GAs promote juvenile to adult transition in *Arabidopsis*, as indicated by the increase in endogenous GA levels during the transition (Andrés et al. 2014) and by the induction of the differentiation of trichomes on the abaxial surface of leaves by GA treatments (Telfer et al. 1997; Gan et al. 2007; Galvão et al. 2012; Porri et al. 2012; Park et al. 2013). GAs also promote the initial step of the transition to the reproductive state when *Arabidopsis* plants are under noninductive short day conditions, but have little effect when plants are under inductive longday conditions (Hedden and Kamiya 1997; Yamaguchi 2008; Mutasa-Göttgens and Hedden 2009). It is noteworthy that the exogenous application of GAs is able to directly activate the transcription of the LFY gene, whose direct target is AP1 (Blázquez et al. 1997, 1998, see also Fig. 2). Both genes are necessary for flower formation in *Arabidopsis* (Weigel et al. 1992; Blázquez et al. 1997, 1998). Accordingly, *lfy ap1* double mutants are able to perform the first stage of vegetativetoreproductive phase transition, and thus inflorescence meristems are produced, but floral meristems do not complete their development (Weigel et al. 1992).

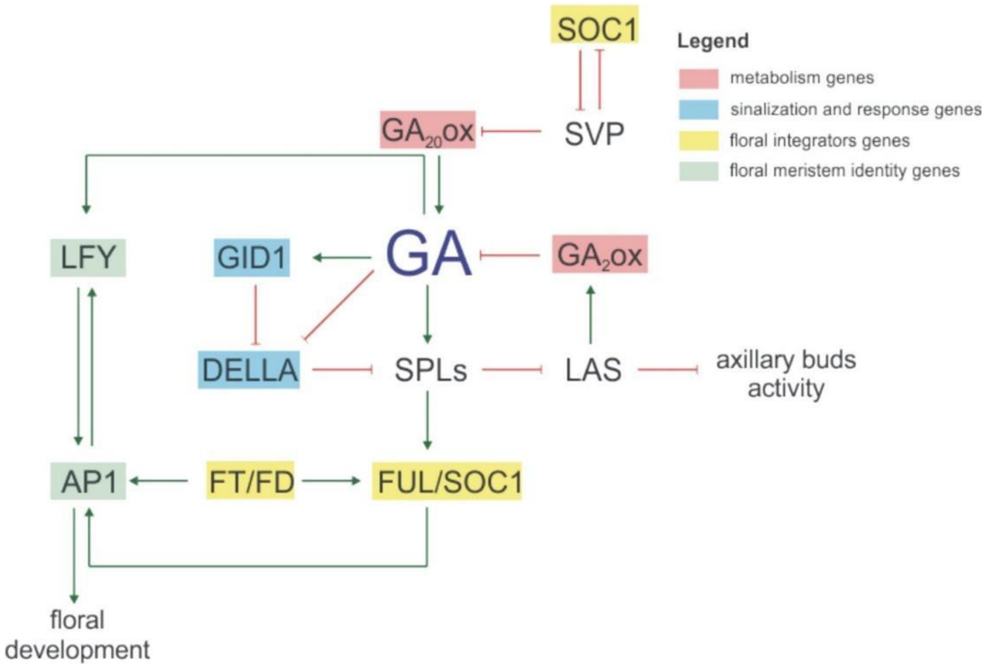

Figure 2. Model of interactions between GA and genes involved in phase transitions. Adapted from Andrés et al. (2014), Hedden and Kamiya (1997), Hyun et al. (2016), Porri et al. (2012), Yamaguchi et al. (2014) and Zhang et al. (2020)

Under low GA concentrations, a DELLA protein associates to the regulatory region of *SPL15* repressing its transcription and thus indirectly repressing the activation of miR172 and *FUL* (Hyun et al. 2016). As SPL15 promotes the first step of reproductive development (the switch from vegetative to the inflorescence meristem), a rise in GA levels induces the degradation of DELLA and the release of SPL15 to activate the expression of *FUL* together with SOC1 (Yamaguchi et al. 2014; Wagner 2016; Hyun et al. 2016, see also Fig. 2). On the other hand, a close paralog to *SPL15*, *SPL9* also promotes the reproductive development, but it acts at a second, later stage: the differentiation of floral meristems (Yamaguchi et al. 2014; Wagner 2016). In this case, as SPL15 recruits DELLA to the regulatory region of *FUL*, SPL9 recruits DELLA to the promoter of AP1, which is a MADS-box gene encoding a transcription factor closely related to FUL (Yamaguchi et al. 2014; Hyun et al. 2016). Interestingly how ever, instead of repressing transcription (as it happens with SPL15/DELLA), the association of SPL9 and DELLA activates the transcription of *AP1* (Yamaguchi et al. 2014; Hyun et al. 2016), in a pathway that is parallel to the one described above for the GA-mediated activation of *LFY/AP1* (Fig. 2). Thus, this explains why GAs induce the first step of reproductive development (the transition from the vegetative meristem to the inflorescence meristem), but repress the sec ond step (flower formation). Intriguingly, this mechanism seems to be at least partially conserved (Ahsan et al. 2019;

Jameson and Clemens 2019) and may also be involved with the general perception that for some plants GAs induce flowering while in other species they repress flowering, as exogenous applications of GAs might have opposite effects depending on the exact moment the treatment was applied. This might be particularly troubling for homoblastic tropical species whose exact developmental stage (juvenile versus adult vegetative) is hard to predict based on morphology only (see above the section on morphological markers of phase change).

In a pathway parallel to the one described above, FLC and SVP delay flowering by suppressing the expression of target genes such as *FT* and *SOC1* (Fig. 2). While FLC regulates the expression of these genes in leaves, SVP acts at the shoot apex (Mateos et al. 2015). SVP directly control GA levels in the vegetative meristem by repressing the expression of *GA20OX2*. Accordingly, GA levels are high in svp mutants (Andrés et al. 2014; Mateos et al. 2015). Although the influ ence of GAs in *Arabidopsis* plants under long days is reduced, GAs activate the expression of FT in leaves, thus interfering with the FT/FD complex formation (Porri et al. 2012; Conti 2017, see Fig. 2).

Additionally to their role in modulating flowering per se, GAs are also known to regulate the outgrowth of axillary meristems, thus controlling plant architecture (see the review by Eshed and Lippman 2019). As for *Arabidopsis*, in most plants the transition to the adult stage involves the activation of axillary meristems (Han et al. 2014; Wagner 2016). The activity of axillary meristems also greatly modifies inflores cence architecture (Benlloch et al. 2007). Recently, it has been shown that the underlying molecular mechanism involves the participation of the *miR156*-targeted *SPL9* gene (Zhang et al. 2020). Alternatively, either miR156 or DELLA proteins re press the activity of SPL9, which in turn represses the expres sion of *LATERAL SUPPRESSOR (LAS)*, a key gene in the initiation of axillary meristem development (Greb et al. 2003). By its turn, LAS induces the expression of *GA2OX4* in the axils of leaves, creating an anatomically limited region of low concentration of bioactive GAs, activating axillary meristem growth (Zhang et al. 2020). Thus, exogenous treat ment with GAs or increasing local GA levels by ectopic ex pression of the GA biosynthesis gene *GA20OX2* inhibits ax illary meristem activation (Zhang et al. 2020). Bellow we will see that much of the control of axillary meristem activity exerted by GAs might be under crosstalk influence by CKs.

Molecular aspects of the influence of CKs in phase transition and plant architecture

Cytokinins are a group of phytohormones that regulate several aspects of plant growth and development including repression of senescence and stimulation of both cell division and lateral bud activity (Chen 1997; Sakakibara 2010; D'Aloia et al. 2011). Two classes of enzymes perform CK biosynthesis: ISOPENTENYL TRANSFERASE (IPT) and LONELY GUY (LOG) (Chen 1997). Most of the cytokinins that occur naturally derive from N6-isopentenyladenin (iP) (Sakakibara 2006). CYP735A enzymes catalyze the conversion of iP in transzeatin (tZ) (Yamburenko et al. 2017). iP carries an intact isopentenyl side chain while tZ and ciszeatin (cZ) carry hydroxylated side chains (Miyawaki et al. 2006). The degradation of cytokinins, in turn, is catalyzed by cytokinin oxidases/ dehydrogenases (CKXs) (Bartrina et al. 2011). Cytokinin signal transduction begins with the autophosphorylation of a membranebound receptor, CYTOKININ RESPONSE1 (CRE1)/AHK4, and a phosphorylation cascade involving the *ARABIDOPSIS* HISTIDINE PROTEINS (AHPs) and *ARABIDOPSIS* RESPONSE REGULATORS (ARRs).

The interaction of a cytokinin molecule with its receptor triggers a phosphorylation of the AHPs (Li et al. 2010) which are translocated to the nucleus, where the type-B ARRs (CK response activators) or type-A ARRs (CK response repressors) are activated (Bhargava et al. 2013).

Cytokinins influence phase transitions by meristem regulation, promoting cell divisions and flowering stimulation (Gordon et al. 2009; Li et al. 2010; Tarkowská et al. 2019; Wu et al. 2019). Applying exogenous CKs to *Arabidopsis* plants under noninductive short days induced flowering (D'Aloia et al. 2011). Additionally, CK treatment induced an increase in the transcription of the *TWIN SISTER OF FT (TSF),* a close paralog of *FT*, while *FT* levels did not change, suggesting that TSF might replace FT functions while stimulating flowering under noninductive conditions probably in association with SOC1 (D'Aloia et al. 2011, Conti 2017; see also Fig. 2). When CK levels were locally increased in floral meristems by overexpressing the CK biosynthesis gene *AtIPT4* under the control of the *AP1* promoter, enlarged inflorescence and floral meristems were produced (Li et al. 2010). This phenotype was attributed to signaling by AHK2 and AHK3 that led to an increase in the expression of effector genes such as *CUP-SHAPED COTYLEDON* (*CUC2* and *CUC3*) (Li et al. 2010). The *CUC1, CUC2* and *CUC3* genes are partially redundant (Aida et al. 1997; see Fig. 3) and are related to the establishment and maintenance meristems through the promotion of the *SHOOT MERISTEMLESS* (*STM*) gene (Laufs et al. 2004).

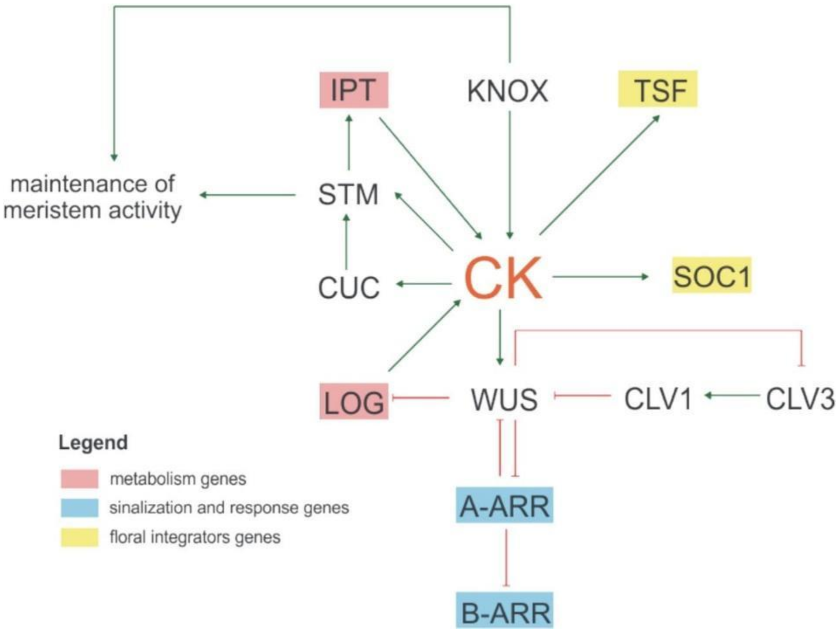

Figure 3. Model of interactions between CK and genes involved in phase transitions. Adapted from Azarakhsh et al. (2015), Bartrina et al. (2011), Gordon et al. (2009), Howell et al. (2003), Kieber and Schaller (2018) and Li et al. (2010)

STM acts complementarily to WUSCHEL (WUS) in regulating *Arabidopsis* shoot meri stem activity (Lenhard et al. 2002). WUS modulates the rate of meristem growth by antagonistically interacting with the *CLAVATA* (*CLV*) genes and it has been proposed that CKs stimulates *WUS* and represses *CLV* expression (Gordon et al. 2009). Additionally, WUS represses the activities of type-A ARRs enhancing CK signaling and creating a feedback loop (Leibfried et al. 2005). This regulatory mechanism can be extended to axillary meristems as CKs promote axillary meristem indeterminancy and affect inflorescence architecture by promoting expression of *WUS* and repressing *CLV1* and *CLV3* (Han et al. 2014; Fig. 3). Finally, *Arabidopsis* plants overexpressing type-A ARRs have an early flowering pheno type and show altered expression not only of FD, LFY, and TSF, but also increased *GA1* transcriptional activity (Wu et al. 2019). These results suggest that CKs play a critical role in modulating flower initiation not only by affecting the photo periodic and autonomous pathways, but also by interfering with GA signaling, indicating an important interplay between GA and CK pathways.

Crosstalk between GA and CK pathways

The crosstalk between GA and CK pathways occur at different molecular levels. On one hand, CK activity is required and sufficient to stimulate the expression of *GA2OX* (Jasinski et al. 2005) indicating that CKs interfere with GA biosynthesis. On the other hand, molecules involved with CK signaling such as ARRs are able to bind DELLA proteins, indicating that CKs also interfere with GA signaling. However, unlike most cases were DELLAs act as transcriptional repressors, ARR/DELLA complexes generally relocate to the promoter of the target genes, inducing their expression (Marín-de la Rosa et al. 2015; Conti 2017).

Although most of the molecular mechanisms involved still remain largely unknown, both GA and CK signaling path ways are modulated simultaneously by genes related to the establishment of SAM and floral development such as *KNOX* (Jasinski et al. 2005) and *BELL* (Dolgikh et al. 2019). *KNOX* genes play several roles in the regulation of plant development, such as initiation and maintenance of shoot meristems, mainly by *STM*, which is a *KNOX* Class I gene (Hake et al. 2004). Jasinski et al. (2005) analyzed the expression of KNOX genes in the SAM of *Arabidopsis* and its effects on CK and GA levels. The authors concluded that not only KNOX proteins modulate CK biosynthesis (e.g. by repressing GA20OX and stimulating GA2OX) but also CK signaling (e.g. by modulating the activity of ARRs, see Fig. 4). Thus, KNOX proteins promote SAM activity by si multaneous activation of CK and repression of GA biosynthe sis and signaling (Jasinski et al. 2005).

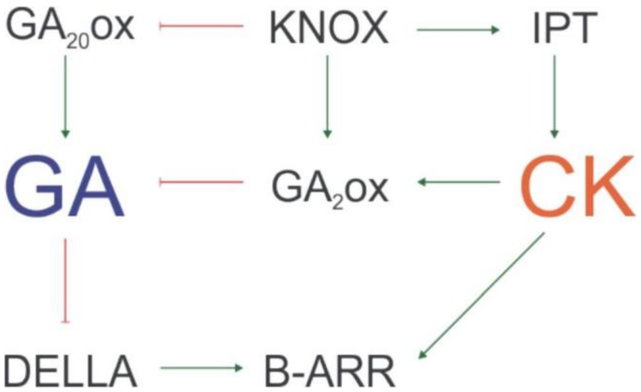

Figure 4. Model of interactions between GA and CK pathways in phase transitions. Adapted from Jasinski et al. (2005) and Weiss and Ori (2007)

Perspectives to manipulate CK and GA levels in tropical species and the conservation of phase change pathways

The perspective of manipulating GAs and CKs endogenous levels in tropical species of economic interest, either through exogenous application of these phytohormones as commer cially available growth modulators or by genetically modify ing their biosynthesis or signaling pathways, might have a great impact in tropical crop yields. The success of this approach relies greatly on the conservation of the molecular pathways involved. So far the literature available on the sub ject is quite optimistic, although some particularities are ex pected to occur (e.g. see the review of Jameson and Clemens 2019 and also Ahsan et al. 2019 and the references therein).

Breeding and improving tropical/subtropical tree crops such as avocado, mango and macadamia (*P. americana*, *M. indica* and *M. integrifolia*, respectively) are hindered by long juvenile phases. Recently, Ahsan et al. (2019) reported that transcription of the equivalent *miR156* putative orthologs in these species decreases as these trees age. Thus, *miR156* levels could be used as a juvenility marker in these species because, as we mentioned earlier, there are no clear morphological markers in these species that would allow the identification that the juvenile to the adult vegetative phase transition occurred.

Consistent with the *Arabidopsis* model, they also observed a conserved regulation of the *miR156-SPL3/4/5* module in all these three phylogeneti cally distant tree crops, suggesting a highly conserved role for this pathway in establishing a vegetative identity (Ahsan et al. 2019). On the other hand, the accumulation of miR172 transcripts and the decrease in its target *AP2-like* genes as well as the upregulation of *SPL9* were not related with plant age in these crops except in avocado, where the levels of miR172 transcripts increased steadily (Ahsan et al. 2019). These observations indicate some divergence from the model described in *Arabidopsis*, what was somehow expected as *Arabidopsis* is an annual spe cies (and thus reproduces only once) and the mentioned tree species are perennial, and thus flower by “flushes” of activation of the axillary meristems once every year (Wilkie et al. 2008).

Therefore, most of the effects of GA in phase change in avoca do, mango and macadamia are interpreted as interferences in axillary bud release and/or direct effects in flower bud sustained development (Salazar Garcia and Lovatt 2000; Davenport 2007;

Wilkie et al. 2008; Jameson and Clemens 2019). Thus, at least in mango and avocado, inhibiting GA biosynthesis (e.g. by exogenous application of paclobutrazol) allows manipulating the timing of “flushes” or release of axillary bud outgrowth (Salazar-Garcia and Lovatt 2000; Davenport 2007; Wilkie et al. 2008). This approach of using artificial inhibitors of GA biosynthesis has improved the time of breeding programs in Eucalyptus by 50% (Griffin et al. 1993; Moncur and Hasan 1994; Hasan and Reid 1995).

As one might expect, applying exogenous GA to either mango, avocado or *Eucalyptus* inflorescences with already developing floral meristems cause floral bud abortion (Salazar Garcia and Lovatt 2000; Wilkie et al. 2008). This phoenomenon was also observed in Citrus (GoldbergMoeller et al. 2013) and *Metrosideros* (Jameson and Clemens 2019). Interestingly, in all the tree species mentioned so far in this section, flowering certainly involves a con served module of various floral genes, including these species’ equivalent orthologs of *AP1* and *SOC1*, which were upregulated in the reproductive phase (Ahsan et al. 2019; Jameson and Clemens 2019). And at least in the case of *Citrus* and *Metrosideros,* this conserved module probably contains a *LFY* ortholog whose expression is modulated by GA (Goldberg Moeller et al. 2013; Jameson and Clemens 2019).

In some tropical and subtropical heteroblastic perenial fruit species such as passion fruit (*Passiflora* spp), the transition from the juvenile to the adult vegetative phase is readily visible by morphological markers such as the presence of tendrils in the adult plant (Cutri et al. 2013). Nonetheless the analysis and interpretation of the degreee of conservation of the mo lecular modules controlling phase transition in passion fruit might be blurred by the fact that the tendrils are considered part of a modified inflorescence in this species and thus, adult vegetative passion fruit plants already express orthologs of *LFY*, *AP1* and *FUL* (Scorza et al. 2017). According to the *Arabidopsis* model, these genes were expected to express only in plants at the reproductive stage (Wagner 2016). Despite these observations, the effects of exogenous GA application to adult passion fruit plants have similar effects to those re ported for the tropical trees shown above: Increase in GA levels causes the abortion of preformed floral meristems (Nave et al. 2010). Accordingly, application of an inhibitor of GA biosynthesis such as paclobutrazol or uniconazole largely increased the production of floral buds and so did the application of Forchlorfenuron (FCF), a synthetic cytokinin (Cutri et al. 2013). Moreover, CK applications provided resis tance do high temperatures in *P. edulis*, promoting flowering even in warm temperatures (34/22 °C day/night) under long photoperiods (Sobol et al. 2014).

This approach of combining the repression of GA biosynthesis and application of exogenous CKs, allowed flower buds to complete development all year round (and thus irrespective to day length) under field conditions and thus allowing fruit production in new seasons (Chayut et al. 2014). Similarly, to study the role of the crosstalk between CKs and GAs in branching and flowering, Subbaraj et al. (2010) conducted an experiment with calla lily, *Zantedeschia* sp. It was observed that the exogenous application of GA itself had no effect on branching but stimulated flowering, while application of CK alone had no effect on flowering but stimulated branching. Therefore, applying CK right after the GA treatment enhanced the overall number of flowers produced, suggesting that the crosstalk between CKs and GAs increased floral productivity (Subbaraj et al. 2010). The ability to manipulate flowering time and at the same time fine tuning productivity and protecting plants from environmental stresses, as shown by the examples above, are highly desirable features for tropical crops that will have to deal with drastic climate changes in a not so distant future.

Conclusions

GAs and CKs endogenous levels have a great impact in plant phase transitions. As the increase of the endogenous levels of GAs is generally related to the end of the juvenile phase, it is widely known that GAs may induce or repress flowering in different plant species. However, our view of the roles of GAs in the vegetative to reproductive phase progression has changed recently with the demonstration that the vegetative to reproductive transition in *Arabidopsis* is a two-step process. While GAs induce the transition from the vegetative to the inflorescence meristem, the levels of GAs have to be reduced in order to maintain flower development. As we are just beginning to understand these processes at the molecular level in model plants, it is becoming more evident that the vegetative to reproductive transition is also a twostep process in nonmodel tropical plants with economical interest. This is certainly a research avenue to be pursued and it might have a considerable impact on the way we perceive the effects of the agricultural use of commercial growth modulators containing GAs and/or CKs. An increasing amount of published evidences points out to the (at least partial) conservation of the molecular key players involved in phase transition and the roles that

GA and CK pathways have in modulating the expression of such players. The knowledge about the crosstalk between GA and CK pathways might allow the finetuning of manipulating plant and inflorescence architectures. This might have a great impact on improving yield and speeding up breeding programs of tropical and subtropical perennial fruit species. Future studies aiming the application of the knowledge generated in model species regarding the control of flowering by GAs and CKs to tropical plants under commercial field conditions would allow us to obtain tropical crops more adapted to future challenging environments.

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CAPÍTULO II - Alterações morfológicas na transição juvenil para adulta vegetativa causadas por citocinina e giberelina em *Passiflora organensis*

Resumo

Os fitormônios citocinina (CK) e giberelina (GA) afetam o desenvolvimento e o crescimento dos vegetais em geral, influenciando diretamente as transições de fases. As espécies do gênero *Passiflora* são bons modelos para estudos de desenvolvimento por apresentarem diferenças claras entre as fases juvenil, adulta vegetativa e adulta reprodutiva. Neste capítulo, buscamos caracterizar as alterações morfológicas ocorridas durante a transição juvenil para adulta vegetativa, em plantas de *P. organensis* submetidas a tratamentos com CK e GA exógenas. Foram aplicados sobre plantas jovens de *P. organensis*, GA_3, uma giberelina bioativa, e benzilaminopurina (BAP) uma citocinina sintética, em experimentos separados, durante duas semanas, em três diferentes doses. A giberelina induziu a formação de gavinhas enquanto a citocinina inibiu. Em relação à morfologia foliar, ambos os reguladores causaram mudanças na morfologia das folhas, porém de maneiras diferentes. A GA causou redução das manchas acinzentadas na face adaxial, alterações na forma, tendo extremidades mais afiladas, mimetizando a morfologia de folhas adultas. A CK em doses mais altas causou deformidades nas folhas. As plantas que receberam CK apresentaram ativação das gemas laterais a partir da primeira semana após a aplicação.

Abstract

Cytokinin (CK) and gibberellin (GA) phytohormones affect the development and growth of plants in general, directly influencing phase transitions. The species of the genus *Passiflora* are appropriate models for development studies as they show clear differences between the juvenile, adult vegetative and adult reproductive phases. In this chapter, we characterized morphological changes that occurred during the juvenile to vegetative adult transition in *P. organensis* plants subjected to treatments with exogenous CK and GA. GA_3, a bioactive gibberellin, and benzylaminopurine (BAP), a synthetic cytokinin, were applied at three different doses to young *P. organensis* plants, in separate experiments, for two weeks. Gibberellin induced tendril formation while cytokinin inhibited it. Regarding leaf morphology, both regulators caused changes in leaf morphology, but in different ways: GA caused a reduction of grayish spots on the adaxial face, changes in shape, with sharper edges, mimetizing the morphology of adult leaves. CK at higher doses caused leaf deformities. Plants that received CK showed activation of the lateral buds after the first week of application.

Introdução

Os fitormônios citocinina (CK) e giberelina (GA) atuam diretamente sobre o crescimento e o desenvolvimento vegetal. Os papéis biológicos mais conhecidos das giberelinas são o alongamento dos entrenós e germinação das sementes (Hedden e Thomas 2012; Taiz e Zeiger 2017). As citocininas, por sua vez, induzem a divisão celular, a atividade de gemas laterais e retardam a senescência foliar, por levarem a um acúmulo de clorofila e aumentarem a conversão de etioplastos para cloroplastos (Sakakibara 2010).

Além destes efeitos, citocininas e giberelinas influenciam diretamente as transições de fases dos vegetais em geral. A primeira transição, da fase juvenil para a adulta vegetativa, é o momento em que é estabelecida a arquitetura das plantas e também quando elas tornam-se aptas a perceberem os sinais ambientais de indução ao florescimento (Gioppato e Dornelas 2021). Alguns estudos vêm sendo realizados com o objetivo de utilizar a regulação hormonal, para alterar a arquitetura de plantas cultivadas com interesse comercial, por exemplo, controlando o crescimento dos ramos em pessegueiros (*Prunus persica)* (Cheng et al. 2021), ou a formação de inflorescências em videiras (*Vitis vinífera*) (Crane et al. 2012; Jung et al. 2014), diminuindo a altura de orquídeas *Phalaenopsis* (Hsieh et al. 2020), produzindo melancias (*Citrullus lanatus* L.) ‘anãs’ com brotos mais curtos (Sun et al. 2020), aumentando a ramificação em macieiras (*Malus domestica*) (Tan et al. 2018) e modulando a formação de ramos vegetativos e reprodutivos em milho (*Zea mays*) e arroz (*Oriza sativa*) (Du et al. 2017). Estes trabalhos utilizam aplicações exógenas dos fitormônios, CK ou GA, para avaliar seus efeitos no fenótipo da planta, ou produzindo transgênicos, através da mutação ou superexpressão de genes relacionados ao metabolismo do fitormônio analisado.

Em algumas espécies, um mesmo meristema axilar pode gerar inflorescências ou estruturas de apoio e crescimento vegetativo, como gavinhas em videiras e maracujazeiros, ou estolões em morangos. Esta plasticidade morfológica do meristema axilar pode ser modulada por um conjunto de estímulos de natureza ambiental e endógena (Monteiro et al. 2021). Neste contexto, várias análises têm sido realizadas com aplicações de CKs ou GAs durante a fase juvenil nestas espécies (Crane et al. 2012; Cezar et al. 2015; Li et al. 2018).

Em videiras, *V. vinifera*, aplicações de citocinina converteram gavinhas em formação em inflorescências (Srinivasan e Mullins 1981; Crane et al. 2012). Além disso, análises de videiras mutantes com inibição de GA, tiveram gavinhas convertidas em inflorescências, demonstrando que as gavinhas em videiras são inflorescências que foram inibidas e seu desenvolvimento necessita de GA (Boss e Thomas 2002). Portanto, gavinhas em videiras são consideradas inflorescências imaturas, como órgãos reprodutivos que apresentam passos sequenciais durante o desenvolvimento (Crane et al. 2012). A partir dos mesmos meristemas axilares, CKs promovem o desenvolvimento de inflorescências enquanto GAs interrompem e, por sua vez, estimulam o desenvolvimento de gavinhas (Claassen 2020).

Em morangos, *Fragaria* spp., aplicações de GA induziram a formação de estolões a partir dos meristemas axilares (Hytönen et al. 2009; Kour et al. 2017; Tenreira et al. 2017; Li et al. 2018). Além das análises morfológicas após aplicação direta do fitormônio sobre as plantas, análises moleculares e de expressão gênica corroboraram a ação do GA sobre a produção de estolões. Mutações no gene que codifica uma proteína DELLA, que reprime a ação do GA, em *Fragaria vesca*, estimularam o desenvolvimento do estolões também (Caruana et al. 2018). Além disso, o GA_3 aplicado em plantas adultas promoveu o crescimento vegetativo, havendo inibição do florescimento (Kour et al. 2017).

Além de regular a transição da fase vegetativa para a reprodutiva, o balanço entre citocininas e giberelinas regula também a arquitetura das plantas na transição da fase juvenil para a adulta vegetativa. Em *Passiflora edulis*, cujo gênero é objeto de análise deste trabalho, a aplicação exógena de giberelina em plantas juvenis antecipou a transição da fase juvenil para a adulta vegetativa, evidenciada pelo surgimento da primeira gavinha, mas não influenciou na passagem para a fase adulta reprodutiva, sendo que o início do florescimento não foi alterado pela utilização de GA_3 (Cezar et al. 2015). Os efeitos de CKs e GAs foram mais estudados em *Passiflora* sobre a transição para a fase reprodutiva, como em *P. edulis* (Cutri et al. 2013, Nave et al. 2010, Santos et al. 2010, Sobol et al. 2014), *P. cincinnata* (Zucareli et al. 2007) e *P. alata* (Leonel e Pedroso 2005). A partir destes estudos, percebeu-se que a aplicação de GA_3 inibiu o florescimento em *P. edulis* (Sobol et al. 2014), enquanto a CK estimulou o florescimento e portanto a transição para a fase adulta reprodutiva (Cutri et al. 2013). No entanto, a influência destes fitormônios sobre a transição da fase juvenil para a adulta vegetativa ainda precisa ser elucidada tanto em seus efeitos morfológicos como moleculares.

Tendo em vista a importância da compreensão dos mecanismos que regulam a passagem da fase juvenil para a adulta vegetativa, no presente capítulo buscamos avaliar os efeitos de CK e GA sobre a morfologia das plantas na transição da fase juvenil para a adulta vegetativa em *Passiflora organensis*.

Material e Métodos

Estabelecimento dos ensaios em casa de vegetação e aplicação dos fitormônios

Os ensaios foram conduzidos em casa de vegetação, do Instituto de Biologia da Unicamp, na cidade de Campinas-SP, entre os meses de outubro de 2018 e março de 2019. As plantas de *P. organensis* utilizadas foram originárias da coleção do Depto de Biologia Vegetal (IB/UNICAMP) obtidas a partir de micropropagação, mantidas em meio MS (Murashige e Skoog 1962) na concentração de 2,15 g/, 30 g/l de sacarose, 0,1 g/l de inositol, e 2,8g/l de Phytagel. O pH do meio foi ajustado entre 5,0 e 6,0 antes de ser realizada autoclavagem. As plantas foram transplantadas para os tubos de ensaio contendo aproximadamente 12 ml do meio de cultura, em capela de fluxo laminar, sendo uma planta por frasco, e permaneceram em sala de crescimento sob fotoperíodo de 12h, fornecido por lâmpadas fluorescentes brancas, em temperatura de 25°C.

Quando houve o desenvolvimento de raízes, as mudas foram aclimatizadas às condições de casa de vegetação de acordo com técnicas tradicionais (Rosa et al. 2016), em vasos com composto orgânico Genesolo, Genefértil® (Composição: Bagaço de cana, palha de café, turfa, rocha calcárea, estercos e camas de aviário, cinzas, resíduo orgânico industrial papel/celulose e resíduo orgânico agroindústrial classe B) sendo transplantadas duas plantas para cada vaso.

Após uma semana, as plantas aclimatizadas receberam diariamente duas aplicações em spray sobre toda a planta, sendo uma pela manhã e outra no período da tarde com as soluções dos reguladores vegetais e o surfactante Tween-20 (duas gotas a cada 100 ml de solução) durante 14 dias consecutivos. O delineamento experimental foi inteiramente casualizado, com 10 plantas por tratamento, distribuídas nas mesas aleatoriamente.

No ensaio para analisar os efeitos da citocinina, foram avaliados quatro tratamentos, nas seguintes concentrações: 0,0 (controle), 1,0, 10,0 e 100,0 μM de 6-benzilaminopurina (BAP) uma citocinina sintética.

Para analisar o efeito da giberelina foram avaliados sete tratamentos: três concentrações de ácido giberélico (GA_3): 1,0, 10,0 e 100,0 μM, três concentrações (1,0, 10,0 e 100,0 μM) de paclobutrazol (PAC), um inibidor da síntese de giberelina, e um grupo controle (que não recebeu aplicações de GA_3 nem de paclobutrazol). As soluções de PAC foram aplicadas diretamente na terra, no dia em que o ensaio foi estabelecido.

As plantas foram observadas e avaliadas quanto à morfologia foliar, altura da planta, atividade das gemas laterais e presença de gavinhas durante as duas semanas de aplicação dos reguladores e também nas duas semanas seguintes.

Ensaios *in vitro*

Para analisar os efeitos da citocinina foi conduzido também um experimento *in vitro*, no qual plantas de *P. organensis* no estágio juvenil, obtidas de micropropagação, foram mantidas em meio MS (Murashige e Skoog 1962), na concentração de 2,15 g/l, 30 g/l de sacarose, 0,1 g/l de inositol, e 2,8g/l de Phytagel, suplementado com 6-benzilaminopurina (BAP) em três concentrações distintas: 1,0, 10,0 e 100,0 μM. As plantas foram transplantadas do meio básico para os meios contendo BAP, em tubos de ensaio contendo aproximadamente 12 ml do meio, sendo uma planta por frasco, e permaneceram em sala de crescimento sob fotoperíodo de 12h, fornecido por lâmpadas fluorescentes brancas, em temperatura de 25°C. Foram utilizadas 40 plantas, sendo dez para cada uma das concentrações de BAP e dez do grupo controle, que não foram suplementadas com o regulador. As plantas foram observadas por um mês a partir da montagem do experimento, quanto ao desenvolvimento de brotos laterais e gavinhas, desenvolvimento das raízes e altura das plantas, embora não tenham sido realizadas análises quantitativas com os dados.

Análise quantitativa das variáveis

A altura das plantas foi medida no dia do início da aplicação dos fitormônios e após uma semana de aplicação, utilizando uma régua graduada. Os valores obtidos foram submetidos a análises estatísticas utilizando o software R-4.0.5 (R Core Team). Os dados foram submetidos a análise de variância (ANOVA) e teste de Tukey com 5% de significância.

As plantas foram também observadas quanto ao surgimento de gavinhas e de brotos laterais após 14 dias da aplicação dos fitormônios.

Resultados e Discussão

Efeitos das aplicações de citocinina no desenvolvimento de *P. organensis*

Os efeitos observados da citocinina exógena, 6-benzilaminopurina (BAP) no desenvolvimento de *P. organensis* foram: atraso no desenvolvimento das gavinhas (Figura 1A-B), alterações na morfologia foliar (Figura 2), ativação das gemas laterais com desenvolvimento de ramos vegetativos (Figura 1C) e atraso no crescimento das plantas.

As plantas que receberam pulverizações de BAP tiveram o surgimento de gavinhas inibido em relação às plantas controle. Na quarta semana após o início da aplicação dos firomônios, surgiram as primeiras gavinhas nas plantas do controle e nas que receberam 1,0µM de BAP (Figura 1A-B). No entanto, as que receberam BAP nas concentrações de 10,0µM e de 100,0µM não apresentavam gavinhas (Figura 1). Na quinta semana após o início do tratamento hormonal, a porcentagem de plantas que apresentavam gavinhas foi menor quanto maior foi a concentração do fitormônio aplicado: 100% das plantas do controle, que não receberam pulverizações do fitormônio, 66% das que receberam 1µm de BAP, 58% das que foram tratadas com 10µm de BAP e apenas 30% das que receberam 100µm de BAP possuíam gavinhas. A partir destas observações, podemos afirmar que a citocinina exógena inibiu a formação de gavinhas em *P. organensis*, tendo causado atraso em seu surgimento. Como estas observações foram feitas na quinta semana e as plantas foram pulverizadas com as soluções dos reguladores por duas semanas, elas tiveram três semanas para ajustar seu metabolismo.

Figura 1. Morfologia de plantas de *Passiflora organensis* , quatro semanas após serem submetidas a diferentes concentrações da citocinina 6-benzilaminopurina (BAP): A. região do ápice; B. plantas com folhas removidas para uma melhor visualização das gemas laterais; C. detalhe de planta submetida à concentração de 100 µM de citocinina com ativação das gemas laterais. Setas vermelhas = gavinhas. Setas brancas = gemas laterais ativas. Barra: 1cm.

Considerando que em *Passiflora*, as gavinhas são um marcador morfológico da passagem da fase juvenil para a adulta vegetativa (Cutri et al. 2013), podemos considerar que as aplicações de BAP causaram atraso nessa transição de fases, ao mesmo tempo em que promoveram a ativação das gemas laterais vegetativas (Figura 1C). A função das citocininas em promover a ativação de gemas axilares e a redução da dominância apical é bastante conhecida (Werner et al. 2001; Ongaro e Leyser 2008; Waldie e Leyser 2018).

As alterações morfológicas nas folhas causadas pelas aplicações de BAP incluíram desaparecimento das manchas acinzentadas na face adaxial (Figura 2A), desenvolvimento do lobo mediano, que normalmente é mais curto que os demais (Brasileiro 2014), tornando as folhas trilobadas (Figura 2B), e nas concentrações de 10,0µM e de 100,0µM, algumas folhas apresentaram deformações (Figura 2C).

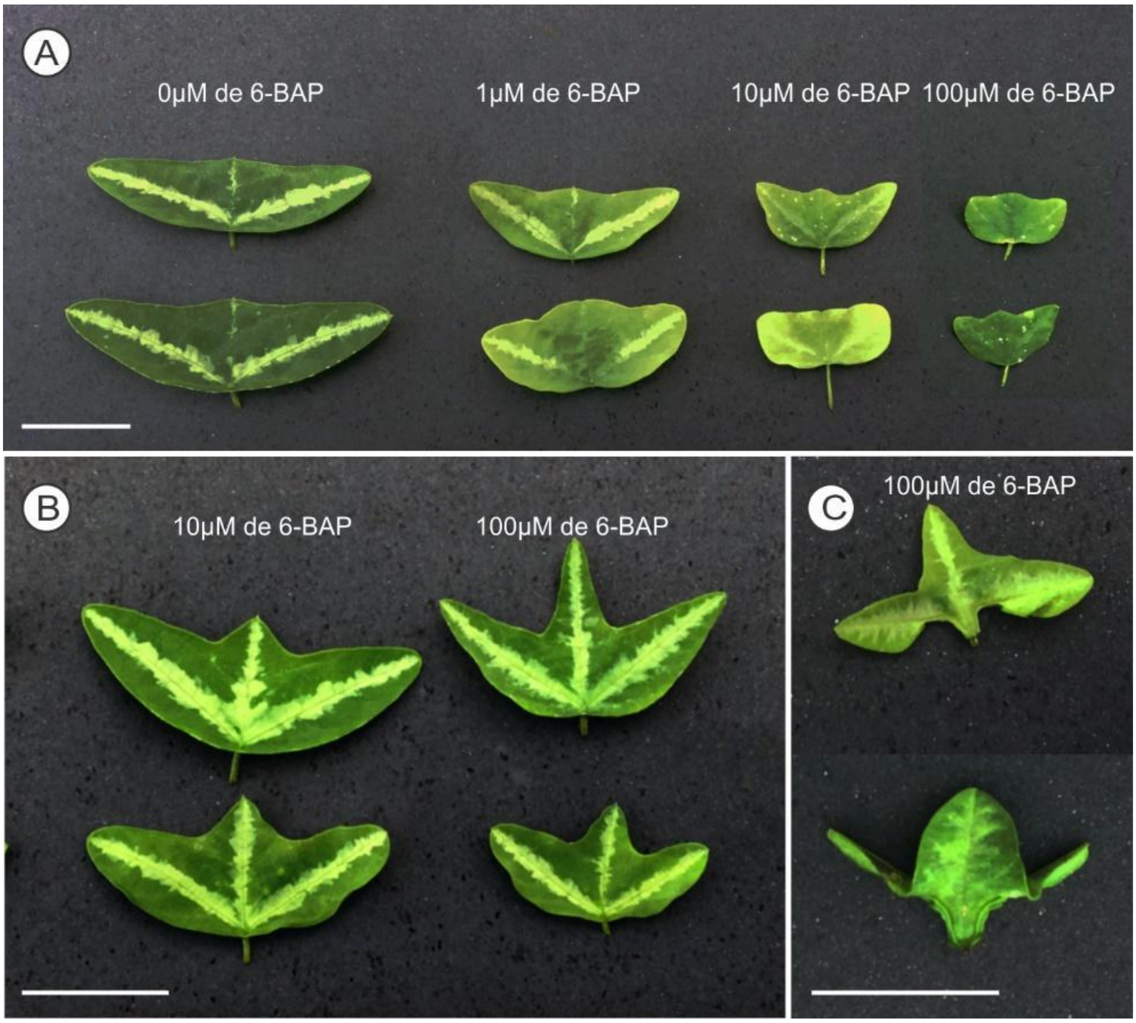

Figura 2. Morfologia foliar de plantas de *Passiflora organensis* submetidas a diferentes concentrações da citocinina 6-benzilaminopurina (BAP). Folhas do terceiro plastocrono coletadas após três semanas de aplicações: A. diferenças quanto à presença de manchas acinzentadas; B. folhas das plantas submetidas às concentrações de 10 e 100 µM de citocinina com lobo mediano mais proeminente; C. folhas das plantas submetidas a 100 µM de citocinina com deformidades. Barra: 1cm.

Portanto, a aplicação de citocinina inibiu a formação de gavinhas em *P. organensis*, mas, por outro lado, estimulou o desenvolvimento de características adultas nas folhas, como a redução das manchas acinzentadas e o desenvolvimento do lobo mediano das folhas. Dentre os vários papéis das citocininas no desenvolvimento vegetal está a regulação da morfologia foliar. Esta regulação ocorre por meio do controle de genes que agem diretamente no desenvolvimento das folhas, como os *KNOX* e *WUSCHEL*, sendo que o aumento da concentração de citocininas leva à formação de folhas profundamente lobadas em monocotiledôneas da família Araceae (Wu et al. 2021) e de folhas compostas em tomateiro, *Solanum lycopersicum* (Shani et al. 2010). Portanto, a influência das citocininas na morfologia foliar durante o desenvolvimento vegetal é conhecida.

Em relação à altura das plantas, as que receberam aplicações de 100µm de CK tiveram visivelmente um crescimento menor após sete dias em relação ao observado no controle. Contudo, os valores médios da altura das plantas não apresentaram diferenças significativas pelo teste de Tukey (Figura 3).

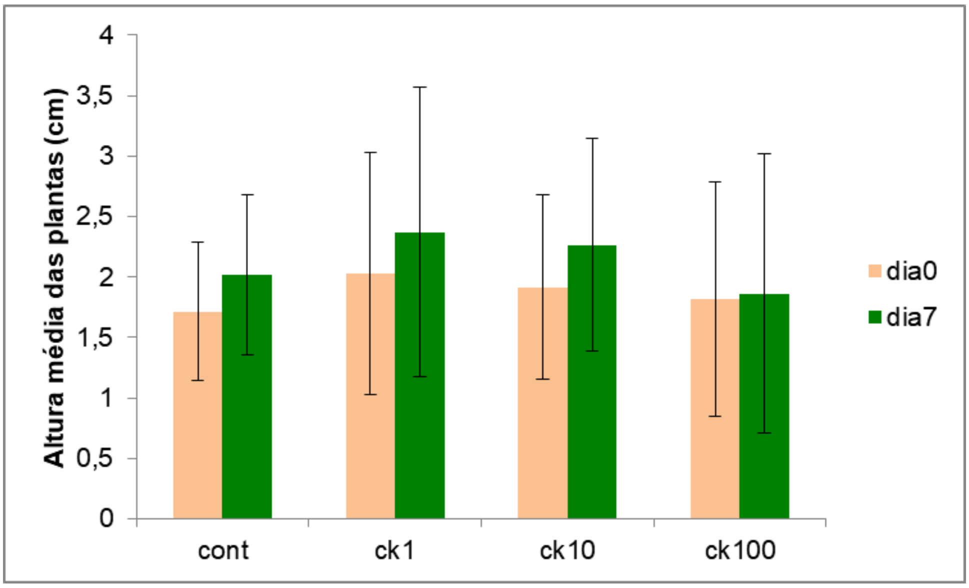

Figura 3. Altura em cm das plantas de *P. organensis* no dia de início da aplicação da CK e após 7 dias consecutivos de aplicações diárias. Não houve diferenças estatisticamente significativas entre as medidas do dia 7 e do dia 0 pelo teste de Tukey (p<5%).

As plantas cultivadas *in vitro* apresentaram diferenças consideráveis quanto à altura, o surgimento de ramos laterais e o desenvolvimento das raízes. Após um mês do experimento, as plantas do grupo controle apresentaram maior altura, desenvolvimento de raízes e não possuíam ramificações laterais (Figura 4). Na concentração de 0,1 µM de BAP, a maior parte das plantas apresentou raízes e um a três ramos laterais. Com 1,0 µM de BAP, a maioria não desenvolveu raízes, sendo formado um calo no local, e apresentaram de três a quatro ramos. Todas as plantas que foram cultivadas com as doses mais altas de BAP, 10,0 µM, tiveram formação de calos no lugar das raízes, tamanho reduzido em relação aos outros tratamentos, sobretudo em relação ao controle, e apresentaram de quatro a seis ramos (Figura 4). A formação de calos (Dubey et al. 2020) e a repressão do desenvolvimento das raízes (Aloni et al. 2004) são efeitos conhecidos das citocininas.

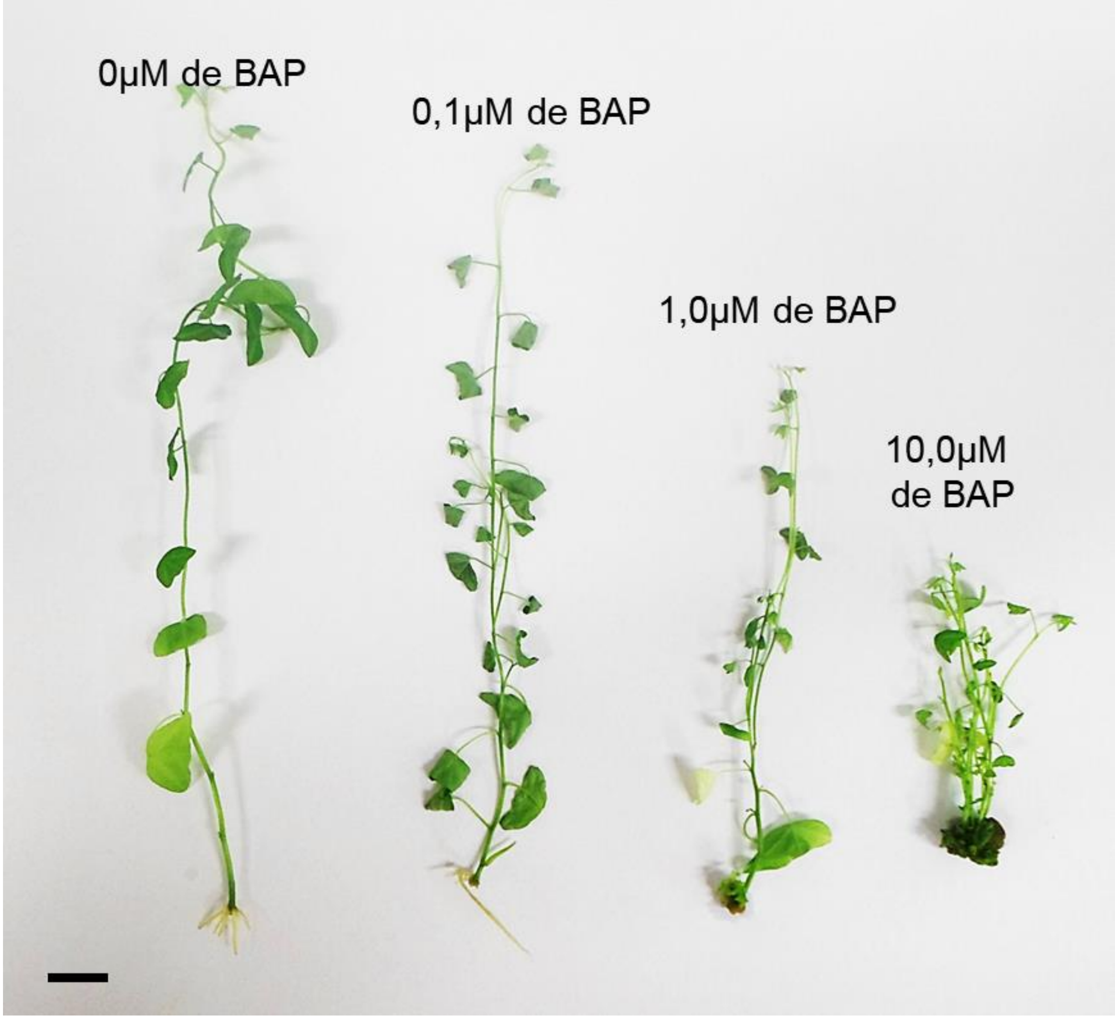

Figura 4. Morfologia foliar de plantas de *Passiflora organensis* cultivadas in vitro após um mês em meios com diferentes concentrações da citocinina benzilaminopurina (BAP). Barra: 1cm.

Efeitos das aplicações de giberelina no desenvolvimento de *P. organensis*

As pulverizações de GA_3 promoveram o surgimento das gavinhas, sendo mais rápido quanto maior foi a concentração do hormônio aplicado; desenvolvimento de folhas com características da fase adulta e o crescimento acelerado das plantas. O paclobutrazol por sua vez inibiu o surgimento das gavinhas e de folhas com características adultas, bem como causou atraso no crescimento das plantas.

Após duas semanas de aplicações de giberelina, as plantas do controle apresentavam a maioria das folhas com manchas acinzentadas e não apresentavam gavinhas (Figura 5). As que receberam aplicações de giberelina apresentavam folhas com morfologia característica da fase adulta (Figura 6) e gavinhas (Figura 5), sendo que estas características surgiram mais precocemente quanto maior foi a concentração do fitormônio. Enquanto as que receberam o paclobutrazol, inibidor da síntese de giberelina, pelo contrário, tiveram atraso no crescimento e no desenvolvimento (Figura 5) sendo estas características mais intensas quanto maior a concentração da substância.

Figura 5. Morfologia de plantas de *Passiflora organensis* submetidas a diferentes concentrações de Paclobutrazol e GA_3: A. plantas submetidas a três concentrações de Paclobutrazol (PAC); B. plantas submetidas a três concentrações de GA_3. Setas vermelhas = gavinhas. Barra: 1cm.

As plantas que foram tratadas com GA_3 na concentração de 1,0µM, ainda apresentavam a mancha acinzentada nas folhas (Figura 5), mas algumas plantas já apresentavam gavinhas. As que receberam 10,0µM de GA_3 estavam com folhas amareladas, sem as manchas, e apresentavam gavinhas. Com 100,0µM de GA_3, todas as plantas apresentavam gavinhas e as folhas estavam sem as manchas acinzentadas

(Figura 6). Além disso, em relação à forma das folhas, as que receberam aplicações de GA_3 apresentavam folhas com lobos mais agudos, sendo esta característica mais intensa nas que receberam 100,0µM de GA_3, a maior concentração do fitormônio (Figura 6).

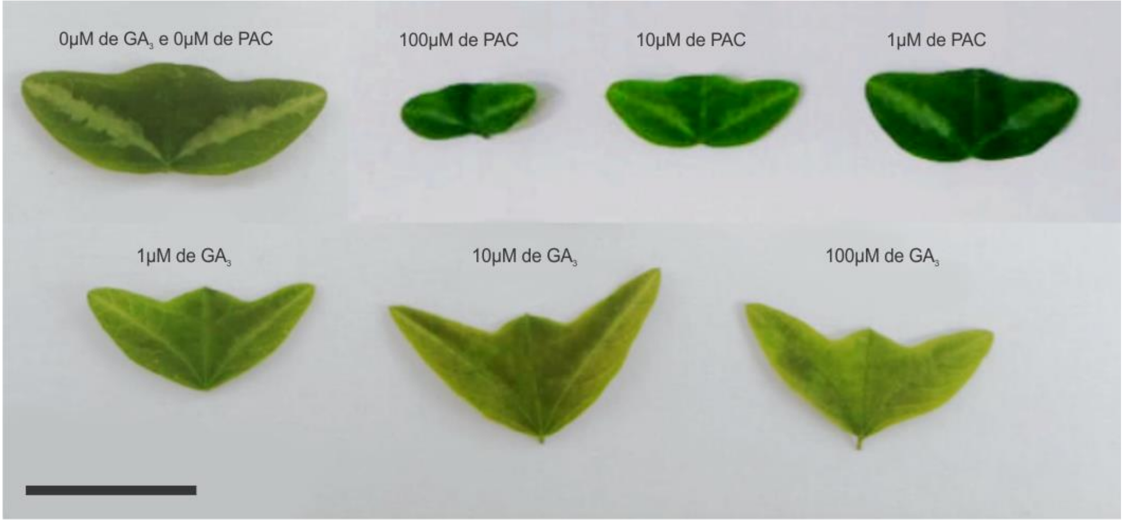

Figura 6. Folhas do terceiro plastocrono de *P. organensis* coletadas após três semanas de tratamento evidenciando as diferenças morfológicas com as diferentes doses de giberelina (GA_3) e de paclobutrazol (PAC). Barra: 1cm.

Por outro lado, das plantas que receberam a aplicação de PAC nenhuma apresentava gavinhas, e todas as folhas continham as manchas acinzentadas, coloração verde escura e forma mais característica da fase juvenil com lobos arredondados (Figura 6). As folhas do controle (0µM de GA_3 e 0µM de PAC) apresentavam forma e coloração intermediária em relação às tratadas com GA_3 e com PAC (Figura 6).

Em relação ao surgimento de gavinhas, a ação da giberelina foi totalmente oposta à da citocinina. Após duas semanas de pulverizações de GA_3, nenhuma planta do grupo controle (que não recebeu aplicações de GA_3), bem como nenhum dos tratamentos com paclobutrazol (PAC) apresentou gavinhas. Contudo, em todos os tratamentos com GA_3 havia plantas com gavinhas, sendo a porcentagem de plantas com gavinhas mais elevada quanto maior a concentração de GA_3 aplicada: 33% das plantas que foram pulverizadas com GA_3 na concentração de 1,0µM, 70% das que receberam 10,0µM de GA_3 e 100% das que receberam pulverizações com 100,0µM de GA_3 apresentavam gavinhas já na segunda semana após o tratamento hormonal.

A giberelina exógena interferiu claramente na altura das plantas, sendo que as que receberam aplicações de 10µM de GA_3 e 100µM de GA_3 tiveram seu crescimento acelerado. Após sete dias da aplicação do fitormônio, as médias das alturas foram significativamente maiores em relação às médias no dia inicial da aplicação, apenas nestes tratamentos (Figura 7).

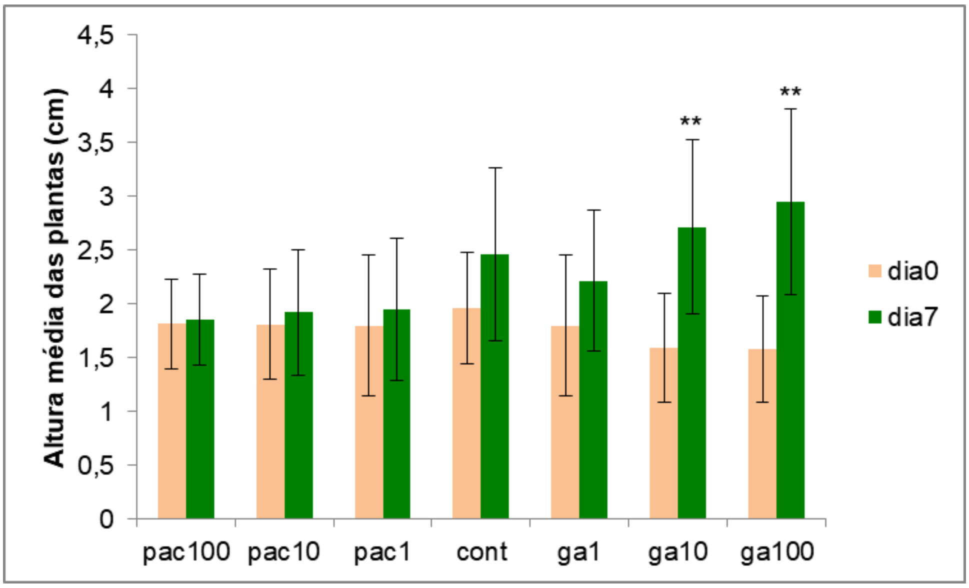

Figura 7. Altura em cm das plantas de *P. organensis* no dia de início da aplicação da GA_3 e após sete dias consecutivos de aplicações diárias. Os (**) indicam diferença estatisticamente significativa entre as medidas do dia 7 e do dia 0 pelo teste de Tukey (p<5%).

O incremento na altura das plantas é um dos efeitos mais conhecidos da giberelina, tendo sido relatado em outras espécies, inclusive do gênero *Passiflora* (Santos et al. 2010; Leonel e Pedroso 2005). Para os outros tratamentos, não houve diferenças significativas no crescimento pelo teste de Tukey (Figura 6), sendo que as plantas tratadas com PAC foram as que tiveram, visivelmente, menor crescimento. Considerando que o PAC é um dos mais potentes repressores de crescimento em vegetais (Jabir et al. 2017), este efeito sobre a altura das plantas era esperado.

Em *Passiflora edulis*, este aumento no crescimento do caule foi crescente quanto maior foi a dose de GA_3, até determinada concentração (de 96 mg/L de solução) (Santos et al. 2010). Contudo, após esta concentração, houve uma rápida diminuição no crescimento, possivelmente devido à superdosagem, sendo este efeito já observado em *P. alata* (Leonel e Pedroso 2005).

Possíveis interações entre citocinina e giberelina na transição juvenil-adulta vegetativa

A plasticidade morfológica foliar em *P. organensis*, é uma característica da espécie. Segundo Milward-de-Azevedo e Baumgratz (2004), a forma da folha pode variar de acordo com as condições ecológicas, pois as folhas podem ser bilobadas com lobos agudos em florestas pluviais; bilobadas com lobos obtusos e mais centrados no cerrado; ou ainda, trilobadas ou bilobadas com lobos arredondados em floresta atlântica. No caso das plantas do presente estudo, as diferenças morfológicas observadas nas plantas submetidas às pulverizações de CK, possivelmente foram devido à superdosagem do regulador, considerando que os hormônios endógenos influenciam nas respostas obtidas (Cato 2006). Portando, as aplicações de CK podem ter causado uma repressão da transição da fase juvenil para a adulta vegetativa, e portanto do surgimento das características adultas.

As alterações foliares causadas pela giberelina estariam relacionadas à antecipação da transição da fase juvenil para a adulta vegetativa, pois as folhas das plantas que receberam aplicações de giberelina são características de folhas adultas. O fato de as que receberam maiores concentrações de GA_3 terem ficado amareladas e senescentes podem ter duas explicações: o aumento da giberelina iria reprimir a citocinina que é responsável por inibir a senescência (Gan e Amasino 1995; Zwack e Rashotte 2013); ou o aumento da giberelina causaria uma redução na fotossíntese e diminuição do acúmulo de clorofila nas células (Li et al. 2010). O paclobutrazol por sua vez, manteria as folhas com uma coloração mais verde escura devido ao acúmulo de clorofila nas células (Xia et al. 2018; Mahulette et al. 2020). Em orquídeas *Phalaenopsis*, a superexpressão do gene OsGA2ox6, de degradação de GA, resultou em plantas com folhas verde escuras, mais curtas e mais largas do que as não transgênicas, demonstrando que a GA influencia na concentração de clorofila e na morfologia das folhas (Hsieh et al. 2020).

As gavinhas surgiram diversas vezes em diferentes grupos de Angiospermas e por isso possuem diferentes origens evolutivas (Sousa-Baena et al. 2018). Em *Passiflora*, bem como em *Vitis vinifera*, as gavinhas são originadas de inflorescências modificadas, sendo que em *Passiflora*, um mesmo meristema axilar da folha divide-se e origina uma gavinha e uma ou mais inflorescências (Nave et al. 2010; Scorza et al. 2017), enquanto em *V. vinifera*, um meristema axilar origina uma única estrutura, podendo ser uma gavinha ou inflorescência (Morrison 1991) de acordo com os estímulos ambientais e endógenos recebidos (Díaz-Riquelme et al. 2014).

Na primeira transição de fases, o surgimento das gavinhas marca o início da fase adulta vegetativa. Os fitormônios giberelina e citocinina possuem papeis antagônicos nesta fase, considerando que, no presente trabalho, quando aplicou-se GA em plantas de *Passiflora organensis*, surgiram gavinhas a partir dos meristemas axilares mais precocemente, ao passo que, quando se aplicou CK, ocorreu atraso no desenvolvimento das gavinhas ao mesmo tempo em que, a partir dos meristemas axilares surgiram brotos laterais. Seriam necessárias análises morfológicas adicionais para compreender a natureza destes brotos. Mas, o tratamento com CK *in vitro*, resultou em plantas com mais ramos laterais e menor tamanho. De modo geral, podemos afirmar que a GA estimula a transição da fase juvenil para a adulta vegetativa em *P. organensis*, enquanto a CK inibe esta transição.

As aplicações destes mesmos reguladores na segunda transição de fases, da fase adulta vegetativa para a reprodutiva, tiveram efeitos opostos em *P. edulis*: enquanto a aplicação de CK estimulou o florescimento (Cutri et al. 2013), a GA inibiu o florescimento (Nave et al. 2010; Sobol et al. 2014).

Consideramos que as gavinhas em *Passiflora* são órgãos reprodutivos modificados, tendo a mesma origem ontogenética das inflorescências (Cutri et al. 2013; Sousa-Baena et al. 2018). Segundo Prenner (2014), a gavinha em *Passiflora* seria o término de uma inflorescência, considerando que gavinhas são estruturas determinadas enquanto inflorescências são indeterminadas. Podemos sugerir que, em *Passiflora*, as GAs seriam responsáveis pela determinação dos meristemas axilares na fase adulta vegetativa e, posteriormente, as CKs estimulariam o desenvolvimento das flores. Essa hipótese foi sugerida em *Vitis vinifera*, em que gavinhas seriam inflorescências que teriam seu desenvolvimento interrompido pela aplicação de GA, tornando-se estrututras determinadas (Boss e Thomas 2002).

Conclusões

A giberelina exógena acelerou a transição da fase juvenil para a adulta vegetativa em *Passiflora organensis*, tendo induzido a formação de gavinhas e de morfologia adulta nas folhas, além de ter acelerado o crescimento das plantas. Com a inibição da biossíntese de giberelina pelo paclobutrazol, o crescimento e o desenvolvimento das plantas foram reprimidos. Por outro lado, a citocinina reprimiu esta transição de fases, inibindo a formação de gavinhas, além de ter causado atraso do crescimento e estimulado o desenvolvimento de ramos laterais.

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CAPÍTULO III - Identificação dos genes de metabolismo e resposta citocinina e giberelina em *Passiflora organensis*

Resumo

Citocininas (CKs) e giberelinas (GAs) estão relacionadas a vários aspectos do desenvolvimento vegetal, desencadeando processos que resultam nas transições de fases. Sua atuação ocorre por meio da ativação da transcrição de determinados genes, e pode ser inibida ou estimulada por fatores ambientais e endógenos, ou interações com outros genes. Neste capítulo, identificamos os genes relacionados ao metabolismo (biossíntese e degradação), sinalização e resposta de CKs e GAs, no genoma de *Passiflora organensis*. Analisamos dez famílias gênicas: *ISOPENTENYL TRANSFERASE* (*IPT*) e *LONELY GUY* (*LOG*), que participam da biossíntese de CK; *CYTOKININ OXIDASES/DEHYDROGENASE* (*CKX*), de inativação de CK; *ARABIDOPSIS RESPONSE REGULATORS* (ARRs) do tipo A e do tipo B, de resposta a CK; *GA3OXIDASE* (GA3ox) e *GA20OXIDASE* (GA20ox) de biossíntese de GA; *GA2OXIDASE* (*GA2ox*) de inativação de GA; *GIBBERELLIN INSENSITIVE DWARF1* (*GID1*), de sinalização de GA; e *DELLA*, de resposta a GA. Fizemos uma análise filogenética dos genes candidatos obtidos, em comparação com os ortólogos de *Arabidopsis thaliana* e *Vitis vinifera*. Analisamos também a estrutura gênica, e observamos que de forma geral, as famílias gênicas de *P. organensis* analisadas são similares às de *A. thaliana* em número e estrutura. Algumas sequências conservadas foram identificadas em todas as classes, que necessitam de análises posteriores para esclarecer suas possíveis funções.

Abstract

Cytokinins (CKs) and gibberellins (GAs) are related to several aspects of plant development, triggering processes that result in phase transitions. They act through the activation of the transcription of certain genes, and it can be inhibited or stimulated by environmental and endogenous factors, or interactions with other genes. In this chapter, we identified, in the genome of *Passiflora organensis*, genes related to the metabolism of (biosynthesis and degradation), signaling and response to CKs and GAs,. We analyzed ten gene families: *ISOPENTENYL TRANSFERASE* (*IPT*) and *LONELY GUY* (*LOG*), which participate in CK biosynthesis; *CYTOKININ OXIDASES/DEHYDROGENASE* (*CKX*), of CK inactivation; *ARABIDOPSIS RESPONSE REGULATORS* (*ARRs*) of type A and type B, for CK response; *GA3OXIDASE* (*GA3ox*) and *GA20OXIDASE* (*GA20ox*) of GA biosynthesis; *GA2OXIDASE* (*GA2ox*) of GA inactivation; *GIBBERELLIN INSENSITIVE DWARF1* (*GID1*), for GA signaling; and *DELLA*, of GA response. We performed a phylogenetic analysis to obtained candidate genes, in comparison with *Arabidopsis thaliana* and *Vitis vinifera* orthologs. We also analyzed gene structure and observed that, in general, the analyzed *P. organensis* gene families are similar to those of *A. thaliana* in number and structure. Some conserved sequences were identified in all classes and further analysis is necessary to clarify their putative functions.

Introdução

A atividade do meristema caulinar das plantas é regulada por muitos fatores, incluindo reguladores transcricionais e hormônios vegetais (Xue et al. 2020). Através de estudos com a espécie modelo *Arabidopsis thaliana*, sabe-se que essas diversas vias convergem para regular a transcrição de um pequeno número de genes integradores que promovem a indução floral, sobretudo *FT* e *SOC1* que codificam, respectivamente, as proteínas FLOWERING LOCUS T e SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1 (Andrés et al. 2014). Como visto nos capítulos anteriores, as citocininas (CKs) e giberelinas (GAs) destacam-se como sendo classes de fitormônios que influenciam diretamente as transições de fases.

As CKs foram descobertas por promoverem a divisão celular em plantas cultivadas em meio de cultura (Skoog e Miller 1957). Além de seu papel bem conhecido na divisão e diferenciação celular, as citocininas estão envolvidas em vários processos essenciais à sobrevivência das plantas, como senescência foliar (Kim et al. 2006), regulação do crescimento da raiz (Werner et al. 2003), translocação de nutrientes (Takei et al. 2001), tolerância ao estresse (Argueso et al. 2009) e formação de nódulos em leguminosas (Sasaki et al. 2014).

As principais CKs biologicamente ativas são a isopenteniladenina (iP) e a transzeatina (tZ) (Sakakibara 2006). Mas há também a ciszeatina (cZ) e a dihidrozeatina

(DZ) (Mok e Mok 2001). As vias metabólicas das CKs bem como os mecanismos de ação, sinalização e resposta estão bem elucidadas atualmente. A biossíntese de iP e tZ é catalisada inicialmente por enzimas do tipo isopenteniltransferases (IPTs), que produzem iP ribotídeos a partir de difosfato de dimetilalil (DMAPP) e 5'difosfato de adenosina (ADP) ou 5'trifosfato de adenosina (ATP) (Taya et al. 1978). As enzimas citocromo P450 monooxigenase, família 735, subfamília A (CYP735A) fazem a hidroxilação de iP-ribotídeos em tZ-ribotídeos (Takei et al. 2001). Posteriomente, as enzimas LONELY GUYs (LOGs) convertem os ribotídeos em CKs ativas (Kurakawa et al. 2007; Kuroha et al. 2009). A degradação das citocininas é realizada pelas citocininas oxidase/desidrogenase (CKX) (Schmülling et al. 2003), que desempenham papéis importantes no controle dos níveis de CK nos tecidos vegetais (Cai et al. 2018).

A transdução de sinais de CK e seu mecanismo de ação começam com a autofosforilação de um receptor ligado à membrana do tipo HISTIDINA KINASE (sendo o primeiro descoberto em *Arabidopsis*, são chamados de AHKs), seguida pela ligação da CK e transferência subsequente do grupo fosfato para a histidina presente na proteína de fosfotransferência (AHPs) e, finalmente, aos reguladores de resposta (ARRs) (Bhargava et al. 2013). Os ARRs do tipo B são ativados pela fosforilação e mediam a expressão gênica regulada por CK, incluindo a regulação positiva dos ARR tipo A, que atuam como reguladores negativos na sinalização de citocinina, reprimindo os ARRs do tipo B (Taniguchi et al. 2007; Argyros et al. 2008).

Os processos regulados por CKs ocorrem por meio de interações com outros hormônios vegetais (Vanstraelen e Benková 2012), dentre os quais estãos as GAs. Sabe-se que CKs e GAs exercem regulação antagônica de múltiplos processos de desenvolvimento (Weiss e Ori 2007). As GAs regulam muitos aspectos do crescimento e desenvolvimento das plantas, incluindo germinação de sementes, alongamento do caule, expansão foliar e desenvolvimento de frutos (Fleet e Sun 2005). Suas vias de biossíntese, degradação, sinalização e resposta são também bem conhecidas. As GAs são derivadas do ent-kaureno, e sua síntese inicia-se nos cloroplastos, onde ocorre a conversão de geranilgeranil difosfato em ent-caureno pelas enzimas ent-copalil difosfato sintase (CPS) e ent-caureno sintase (KS) (Hedden e Thomas 2012).

Posteriormente, no retículo endoplasmático, o ent-caureno é convertido em GA12 pelas enzimas ent-kaurene oxidase (KO) e ácido ent-caurenóico oxidase (KAO) (Hedden e Thomas 2012; Yamaguchi 2008). No citoplasma, ocorre, finalmente, a formação das GAs bioativas a partir da GA12 (Sakamoto et al. 2004). São conhecidas apenas quatro GAs bioativas: GA1, GA3, GA4, e GA7 (Hedden e Phillips 2000). Sua formação ocorre por intermédio das enzimas GA20oxidases (GA20ox) e GA3oxidases (GA20ox) enquanto a degradação (ou inativação) é catalisada pelas GA2oxidases (GA2ox) (Hedden e Phillips 2000).

Com relação ao mecanismo de ação, sabe-se que a GA ativa sua via de resposta ligando-se a seus receptores, GID1s (Hirano et al. 2008). O complexo GA-GID1 interage com as proteínas DELLA, repressoras da atividade das GAs, levando à poliubiquitinação das DELLA, e sua posterior degradação pelo proteassoma 26S (Ueguchi-Tanaka et al. 2007). Portanto, as proteínas DELLA, são importantes reguladoras das GAs (Liu et al. 2010).

Até o momento, a maioria dos estudos relacionados à influência de CKs e GAs nas transições de fases, analizando inclusive a concentração e o padrão de expressão dos genes relacionados a metabolismo, sinalização e resposta a esses fitormônios foram realizados em *A. thaliana* (Blázquez et al. 1998; Bartrina et al. 2011; D'Aloia et al. 2011). Análises em outras espécies vêm sendo realizadas mais recentemente, como, *Vitis vinifera*, a videira (Crane et al. 2012) e *Fragaria vesca*, o morango silvestre (Tenreira et al. 2017; Caruana et al. 2018).

As espécies do gênero *Passiflora* são interessantes modelos para o estudo das alterações moleculares na transição da fase juvenil para a adulta vegetativa, por ocorrerem alterações morfológicas notáveis nesta transição (veja o Capítulo II; Krosnick e Freudenstein 2005; Nave et al. 2010; Cutri et al. 2013). Estudos realizados anteriormente em *Passiflora*, analizaram a passagem da fase adulta vegetativa para a reprodutiva (Sobol et al. 2014; Cutri et al. 2013).

Porém, ainda não há análises moleculares relacionando CKs e GAs à transição da fase juvenil para a adulta vegetativa no gênero *Passiflora.* Neste capítulo, buscamos identificar os genes relacionados a metabolismo, sinalização e resposta a CKs e GAs em *P. organensis*, estabelecer relações filogenéticas entre os genes candidatos e os ortólogos de *A. thaliana*, analizar a estrutura destes genes e identificar regiões conservadas que podem ter funções similares às funções previamente reconhecidas em outras plantas, na espécie estudada.

Material e métodos

Identificação de genes candidatos no genoma de *P. organensis*

O genoma de *P. organensis* (Costa et al. *in press*) foi utilizado como fonte de sequências para a identificação de parálogos dos genes relacionados a síntese, degradação, percepção e resposta de citocininas e giberelinas.

As sequências de *P. organensis* dos potenciais parálogos foram identificadas através de buscas utilizando a ferramenta TBLASTN do *National Center for Biotechnology Information* (NCBI) usando os respectivos genes de *A. thaliana* como referência (Apêndice A, Tabela 1). As buscas foram realizadas nas bibliotecas genômicas de *P. organensis* denominadas LB15042 e LB15043. As sequências proteicas de *A. thaliana* foram utilizadas como isca (*query*) para a identificação dos potenciais ortólogos no genoma de *P. organensis* utilizando o algoritmo BLASTp identificadas no banco de dados do NCBI.

Para cada contig identificado com o TBLASTN como descrito acima, utilizou-se o software BioEdit para a obtenção de mapas de restrição mostrando os três possíveis quadros abertos de leitura e, a partir deles, foram identificadas as sequências de aminoácidos e de nucleotídeos dos genes de *P. organensis.* As sequências genômicas de todos os genes obtidos estão no Apêndice B e as sequências proteicas em formato Fasta, no Apêndice D.

As sequências dos genes candidatos obtidas foram novamente comparadas com o banco de dados do National Center for Biotechnology Information (NCBI) utilizando o BLASTp em associação com Phytozome v12.1 (Goodstein et al. 2012) para a detecção de possíveis discrepâncias. Por fim, os ortólogos de *P. organensis* foram nomeados de acordo com os genes com sequencia proteica mais similar em *A. thaliana.* As sequencias gênicas obtidas estão descritas no Apêndice A.

Caracterização da estrutura gênica

Para a identificação da estrutura dos genes foram utilizados o programa AUGUSTUS (Stanke et al. 2004) de predição gênica, e o programa NetPlantGene (Hebsgaard et al. 1996) para a identificação das fronteiras entre introns e éxons. A representação gráfica da estrutura gênica final foi obtida utilizando o software *GSDS 2.0 Gene Structure Display Gene* (Hu et al. 2015).

Análise filogenética

As sequências proteicas obtidas a partir dos genes de *P. organensis* foram comparadas com as da espécie modelo *A. thaliana* e também com sequências de *Vitis vinifera*, isto pelo fato desta espécie também possuir gavinhas, assim como *P. organensis* e ser uma espécie filogeneticamente mais próxima de *P. organensis* que *A. thaliana*. O alinhamento das sequências foi realizado com os softwares MEGA X 10.0.5 (Kumar et al. 2018) e CLUSTAL. Posteriormente foram montadas as árvores filogenéticas usando o método de Neighbor-Joining.

Resultados e Discussão

Filogenia e estrutura dos genes candidatos envolvidos no metabolismo e resposta à citocinina

Família gênica *ISOPENTENYL TRANSFERASES* (*IPT*)

A maioria das citocininas que ocorrem naturalmente são derivadas da isopenteniladenina (iP) (Sakakibara 2006). A iP carrega uma cadeia lateral de isopentenil não modificada, enquanto a transzeatina (tZ) e a ciszeatina (cZ) transportam cadeias laterais hidroxiladas (Miyawaki et al. 2006).

Existem duas classes de IPTs nas plantas: os ATP/ADP-IPTs e os tRNA-IPTs. Os ATP/ADP-IPTs são responsáveis pela maior parte da biossíntese da citocinina do tipo iP e tZ, os tRNA-IPTs são responsáveis pela biosíntese de citocininas do tipo cZ (Miyawaki et al. 2004). Os ATP/ADPIPTs catalisam o passo inicial na principal via para a biossíntese de citocinina: a N6-prenilação de 5'fosfatos de adenosina para formar iP-ribosídeos 5 'fosfatos (Sakakibara 2006). Em *A. thaliana* há sete IPTs dessa classe: AtIPT1 e AtIPT3-AtIPT8 (Takei et al. 2001).

As citocininas podem também ser sintetizadas pela degradação de tRNAs que contêm resíduos de adenilato. Mas em plantas esta via de síntese de citocininas é considerada menos importante, em relação à quantidade produzida, do que a via que usa IPTs dependentes de ATP/ADP (Chen 1997). Em *A. thaliana* há dois IPTs dessa classe: AtIPT2 (Takei et al. 2001) e AtIPT9 (Miyawaki et al. 2004).

Em *P. organensis*, considerando os ortólogos em *A. thaliana*, foram identificados seis *ADP/ATP-IPTs*: *PoIPT3a, 3b, 5, 6, 7* e *8* (Figura 1), contendo apenas um éxon (Figura 2), e dois *tRNA-IPTs*: *PoIPT2* e *9* (Figura 1). Contudo, o *PoIPT2* tinha uma estrutura semelhante ao do *AtIPT2*, com dez éxons (Figura 2) enquanto o *PoIPT9* continha apenas dois éxons (Figura 2). Apesar de ser o ortólogo do *AtIPT9*, que é um *tRNA-IPT*, o *PoIPT9* foi considerado, em busca pelo BLASTP, com sequência e estrutura similar à do *IPT5* de *Populus trichocarpa*, que é um *ADP/ATP-IPT*. Análises de expressão gênica permitirão caracterizar melhor o papel deste gene.

Böttcher et al. (2015) identificaram em *V. vinifera* oito *IPTs*, seis dos quais agrupados com os *ADP/ATP-IPTs* de *A. thaliana*, e dois ortólogos (*VvIPT2*, *VvIPT9*) dos respectivos *tRNA-IPTs* de *A. thaliana*. Porém, um dos genes, identificado nesse trabalho como *VvIPT15*, de número de acesso no NCBI XM_002278900, não pôde ser identificado como um *IPT*.

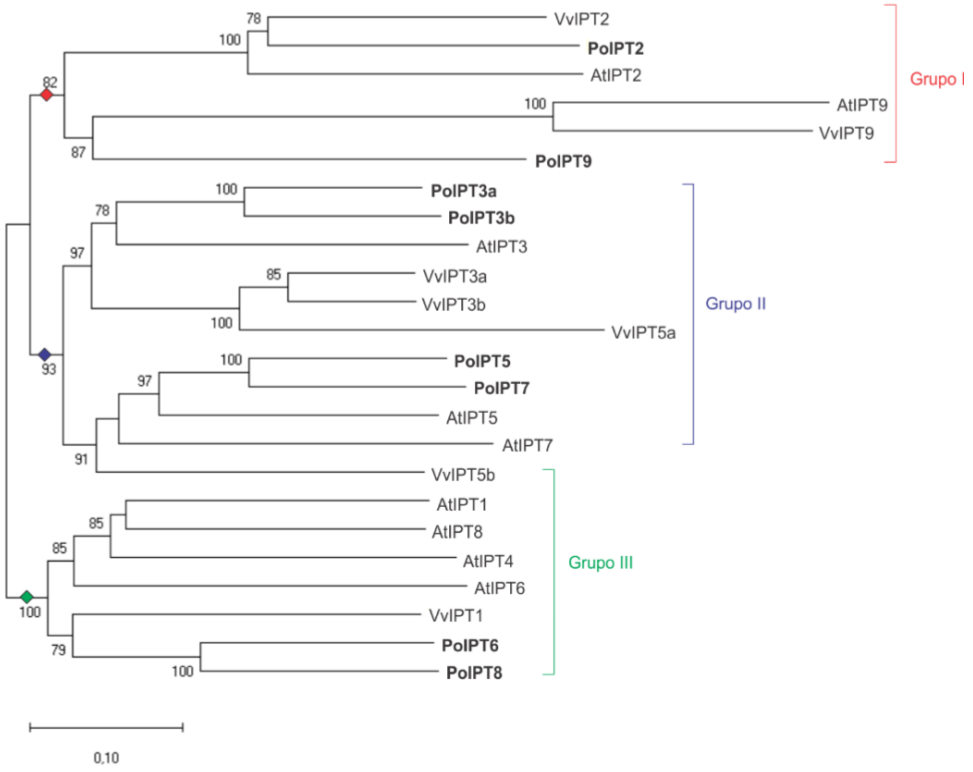


Figura 1. Árvore filogenética da família gênica *IPT* envolvida na síntese de citocinina, contendo genes de *Arabidopsis thaliana* (At) e os ortólogos de *Passiflora organensis* (Po) e *Vitis vinifera* (Vv) O grupo I corresponde aos tRNAIPTs, com base nos ortólogos de *A. thaliana* enquanto os grupos II e III, correspondem aos ATP/ADPIPTs.

A estrutura desta família gênica é conservada em outras espécies, como *A. thaliana* (Miyawaki et al. 2004) (Figura 2), *Brassica rapa* ssp. *pekinensis* (Liu et al., 2013) e *V. vinifera* (Böttcher et al. 2015) (Figura 2). Em geral, os *ADP/ATP-IPTs* apresentam um único éxon ou no máximo dois. Enquanto os *tRNA-IPTs* apresentam em torno de dez éxons e nove íntrons (Figura 2).

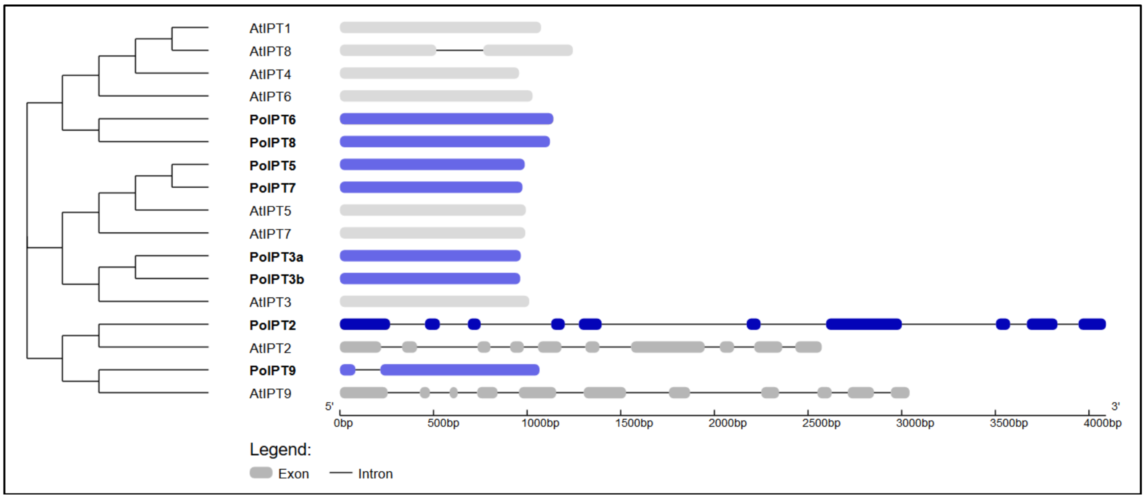
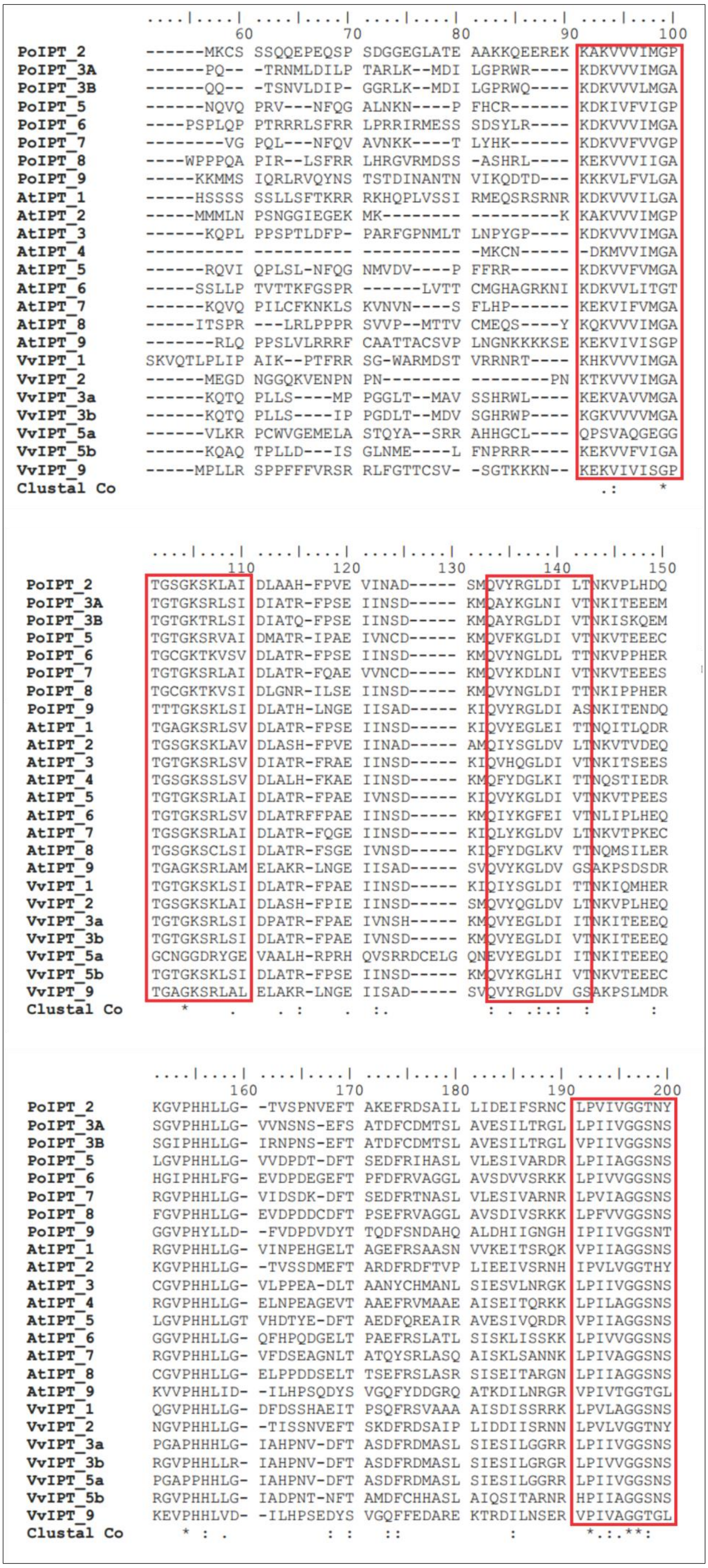


Figura 2. Estrutura dos genes da família IPT Genes em azul são de *Passiflora organensis* (Po) e em cinza de *Arabidopsis thaliana* (At).

O alinhamento das sequências de aminoácidos de IPTs de *P. organensis*, *Arabidopsis* e *Vitis vinifera*, mostrou que apenas algumas características estruturais foram conservadas, sendo identificadas quatro regiões mais similares entre si (Figura 3).



```
                ....|....| ....|....| ....|....| ....|....| ....|....|
                        60         70         80         90        100
PoIPT_2         ------MKCS SSQQEPEQSP SDGGEGLATE AAKKQEEREK KAKVVVIMGP
PoIPT_3A        ------PQ-- -TRNMLDILP TARLK--MDI LGPRWR---- KDKVVVIMGA
PoIPT_3B        ------QQ-- -TSNVLDIP- GGRLK--MDI LGPRWQ---- KDKVVVLMGA
PoIPT_5         ------NQVQ PRV---NFQG ALNKN----P FHCR------ KDKIVFVIGP
PoIPT_6         ----PSPLQP PTRRRLSFRR LPRRIRMESS SDSYLR---- KDKVVVIMGA
PoIPT_7         --------VG PQL---NFQV AVNKK----T LYHK------ KDKVVFVVGP
PoIPT_8         ----WPPPQA PIR--LSFRR LHRGVRMDSS -ASHRL---- KEKVVVIIGA
PoIPT_9         -----KKMMS IQRLRVQYNS TSTDINANTN VIKQDTD--- KKKVLFVLGA
AtIPT_1         -----HSSSS SSLLSFTKRR RKHQPLVSSI RMEQSRSRNR KDKVVVILGA
AtIPT_2         -----MMMLN PSNGGIEGEK MK-------- ---------K KAKVVVIMGP
AtIPT_3         ------KQPL PPSPTLDFP- PARFGPNMLT LNPYGP---- KDKVVVIMGA
AtIPT_4         ---------- ---------- ---------- -MKCN----- -DKMVVIMGA
AtIPT_5         ------RQVI QPLSL-NFQG NMVDV----P FFRR------ KDKVVFVMGA
AtIPT_6         -----SSLLP TVTTKFGSPR ------LVTT CMGHAGRKNI KDKVVLITGT
AtIPT_7         ------KQVQ PILCFKNKLS KVNVN----S FLHP------ KEKVIFVMGA
AtIPT_8         -----ITSPR ---LRLPPPR SVVP--MTTV CMEQS----Y KQKVVVIMGA
AtIPT_9         -------RLQ PPSLVLRRRF CAATTACSVP LNGNKKKKSE KEKVIVISGP
VvIPT_1         SKVQTLPLIP AIK--PTFRR SG-WARMDST VRRNRT---- KHKVVVIMGA
VvIPT_2         ------MEGD NGGQKVENPN PN-------- --------PN KTKVVVIMGA
VvIPT_3a        ------KQTQ PLLS----MP PGGLT--MAV SSHRWL---- KEKVAVVMGA
VvIPT_3b        ------KQTQ PLLS----IP PGDLT--MDV SGHRWP---- KGKVVVVMGA
VvIPT_5a        ------VLKR PCWVGEMELA STQYA--SRR AHHGCL---- QPSVAQGEGG
VvIPT_5b        ------KQAQ TPLLD---IS GLNME----L FNPRRR---- KEKVVFVIGA
VvIPT_9         -----MPLLR SPPFFFVRSR RLFGTTCSV- -SGTKKKN-- KEKVIVISGP
Clustal Co                                                .:    *

                ....|....| ....|....| ....|....| ....|....| ....|....|
                       110        120        130        140        150
PoIPT_2         TGSGKSKLAI DLAAH-FPVE VINAD----- SMQVYRGLDI LTNKVPLHDQ
PoIPT_3A        TGTGKSRLSI DIATR-FPSE IINSD----- KMQAYKGLNI VTNKITEEEM
PoIPT_3B        TGTGKTRLSI DIATQ-FPSE IINSD----- KMQAYRGLDI VTNKISKQEM
PoIPT_5         TGTGKSRVAI DMATR-IPAE IVNCD----- KMQVFKGLDI VTNKVTEEEC
PoIPT_6         TGCGKTKVSV DLATR-FPSE IINSD----- KMQVYNGLDL TTNKVPPHER
PoIPT_7         TGTGKSRLAI DLATR-FQAE VVNCD----- KMQVYKDLNI VTNKVTEEES
PoIPT_8         TGCGKTKVSI DLGNR-ILSE IINSD----- KMQVYNGLDI TTNKIPPHER
PoIPT_9         TTTGKSKLSI DLATH-LNGE IISAD----- KIQVYRGLDI ASNKITENDQ
AtIPT_1         TGAGKSRLSV DLATR-FPSE IINSD----- KIQVYEGLEI TTNQITLQDR
AtIPT_2         TGSGKSKLAV DLASH-FPVE IINAD----- AMQIYSGLDV LTNKVTVDEQ
AtIPT_3         TGTGKSRLSV DIATR-FRAE IINSD----- KIQVHQGLDI VTNKITSEES
AtIPT_4         TGSGKSSLSV DLALH-FKAE IINSD----- KMQFYDGLKI TTNQSTIEDR
AtIPT_5         TGTGKSRLAI DLATR-FPAE IVNSD----- KIQVYKGLDI VTNKVTPEES
AtIPT_6         TGTGKSRLSV DLATRFFPAE IINSD----- KMQIYKGFEI VTNLIPLHEQ
AtIPT_7         TGSGKSRLAI DLATR-FQGE IINSD----- KIQLYKGLDV LTNKVTPKEC
AtIPT_8         TGSGKSCLSI DLATR-FSGE IVNSD----- KIQFYDGLKV TTNQMSILER
AtIPT_9         TGAGKSRLAM ELAKR-LNGE IISAD----- SVQVYKGLDV GSAKPSDSDR
VvIPT_1         TGTGKSKLSI DLATR-FPAE IINSD----- KIQIYSGLDI TTNKIQMHER
VvIPT_2         TGSGKSKLAI DLASH-FPIE IINSD----- SMQVYQGLDV LTNKVPLHEQ
VvIPT_3a        TGTGKSRLSI DPATR-FPAE IVNSH----- KMQVYEGLDI ITNKITEEEQ
VvIPT_3b        TGTGKSRLSI DLATR-FPAE IVNSD----- KMQVYEGLDI VTNKITEEEQ
VvIPT_5a        GCNGGDRYGE VAALH-RPRH QVSRRDCELG QNEVYEGLDI ITNKITEEEQ
VvIPT_5b        TGTGKSKLSI DLATR-FPSE IINSD----- KMQVYKGLHI VTNKVTEEEC
VvIPT_9         TGAGKSRLAL ELAKR-LNGE IISAD----- SVQVYRGLDV GSAKPSLMDR
Clustal Co         *    .   . :    .  :.        : . .:.:  :      :

                ....|....| ....|....| ....|....| ....|....| ....|....|
                       160        170        180        190        200
PoIPT_2         KGVPHHLLG- -TVSPNVEFT AKEFRDSAIL LIDEIFSRNC LPVIVGGTNY
PoIPT_3A        SGVPHHLLG- VVNSNS-EFS ATDFCDMTSL AVESILTRGL LPIIVGGSNS
PoIPT_3B        SGIPHHLLG- IRNPNS-EFT ATDFCDMTSL AVESILTRGL VPIIVGGSNS
PoIPT_5         LGVPHHLLG- VVDPDT-DFT SEDFRIHASL VLESIVARDR LPIIAGGSNS
PoIPT_6         HGIPHHLFG- EVDPDEGEFT PFDFRVAGGL AVSDVVSRKK LPIVVGGSNS
PoIPT_7         RGVPHHLLG- VIDSDK-DFT SEDFRTNASL VLESIVARNR LPVIAGGSNS
PoIPT_8         FGVPHHLLG- EVDPDDCDFT PSEFRVAGGL AVSDIVSRKK LPFVVGGSNS
PoIPT_9         GGVPHYLLD- -FVDPDVDYT TQDFSNDAHQ ALDHIIGNGH IPIIVGGSNT
AtIPT_1         RGVPHHLLG- VINPEHGELT AGEFRSAASN VVKEITSRQK VPIIAGGSNS
AtIPT_2         KGVPHHLLG- -TVSSDMEFT ARDFRDFTVP LIEEIVSRNH IPVLVGGTHY
AtIPT_3         CGVPHHLLG- VLPPEA-DLT AANYCHMANL SIESVLNRGK LPIIVGGSNS
AtIPT_4         RGVPHHLLG- ELNPEAGEVT AAEFRVMAAE AISEITQRKK LPILAGGSNS
AtIPT_5         LGVPHHLLGT VHDTYE-DFT AEDFQREAIR AVESIVQRDR VPIIAGGSNS
AtIPT_6         GGVPHHLLG- QFHPQDGELT PAEFRSLATL SISKLISSKK LPIVVGGSNS
AtIPT_7         RGVPHHLLG- VFDSEAGNLT ATQYSRLASQ AISKLSANNK LPIVAGGSNS
AtIPT_8         CGVPHHLLG- ELPPDDSELT TSEFRSLASR SISEITARGN LPIIAGGSNS
AtIPT_9         KVVPHHLID- -ILHPSQDYS VGQFYDDGRQ ATKDILNRGR VPIVTGGTGL
VvIPT_1         QGVPHHLLG- DFDSSHAEIT PSQFRSVAAA AISDISSRRK LPVLAGGSNS
VvIPT_2         NGVPHHLLG- -TISSNVEFT SKDFRDSAIP LIDDIISRNN LPVLVGGTNY
VvIPT_3a        PGAPHHHLG- IAHPNV-DFT ASDFRDMASL SIESILGGRR LPIIVGGSNS
VvIPT_3b        RGVPHHLLR- IAHPNV-DFT ASDFRDMASL SIESILGRGR LPIVVGGSNS
VvIPT_5a        PGAPPHHLG- IAHPNV-DFT ASDFRDMASL SIESILGGRR LPIIVGGSNS
VvIPT_5b        RGVPHHLLG- IADPNT-NFT AMDFCHHASL AIQSITARNR HPIIAGGSNS
VvIPT_9         KEVPHHLVD- -ILHPSEDYS VGQFFEDARE KTRDILNSER VPIVAGGTGL
Clustal Co         * : .          : :   ::            :        *.:.**:
```

Figura 3. Alinhamentos de regiões das sequências proteicas das PoIPTs, de *Passiflora organensis*, com os AtIPTs, de *Arabidopsis thaliana* e as VvIPTs, de *Vitis vinifera*. A linha

Clustal Co mostra o grau de conservação entre as sequências, sendo representados por [*] os aminoácidos totalmente conservados, [:] altamente conservados e a ausência de símbolos indica que não há conservação entre os resíduos.

Família gênica *LONELY GUY* (*LOG*)

Da família gênica *LOG*, responsável pela ativação das citocininas nas etapas seguintes da biossíntese (Kuroha et al. 2009), foram identificados em *P. organensis* dez genes *LOG* que, em comparação com os de *A. thaliana* e *V. vinifera* puderam ser organizados em quatro clados (Figura 4). Todos eles apresentavam sete éxons (Figura 5). Dois deles, *PoLOG10* e *PoLOG11* não tiveram correspondência com os de *A. thaliana* (Figura 4).

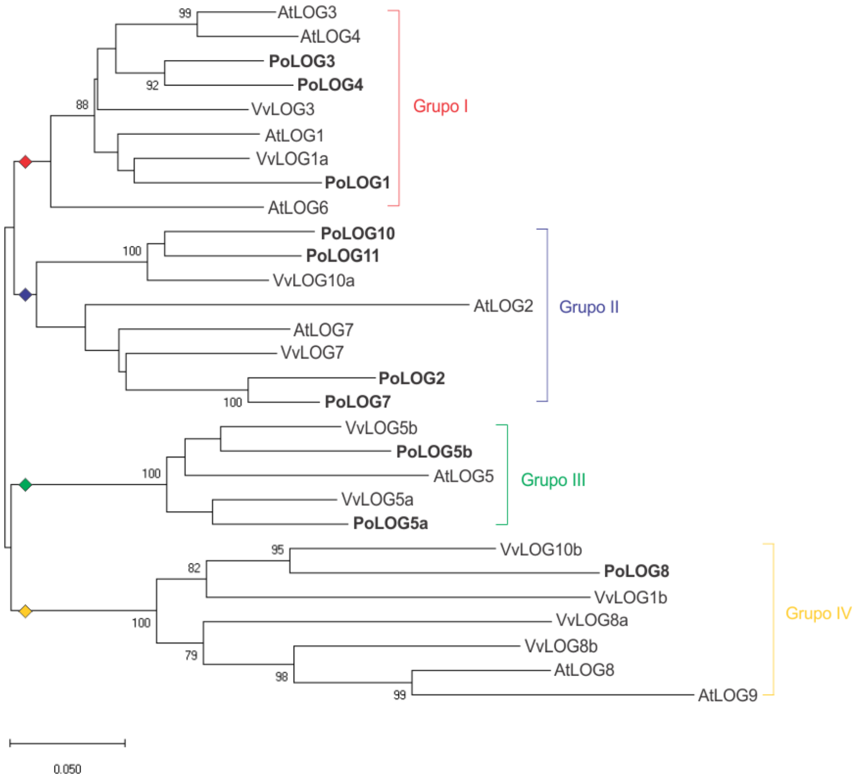


Figura 4. Árvore filogenética da família gênica *LOG* envolvida na síntese de citocinina, contendo genes de *Passiflora organensis* (Po) e os ortólogos de *Arabidopsis thaliana* (At) e *Vitis vinifera* (Vv).

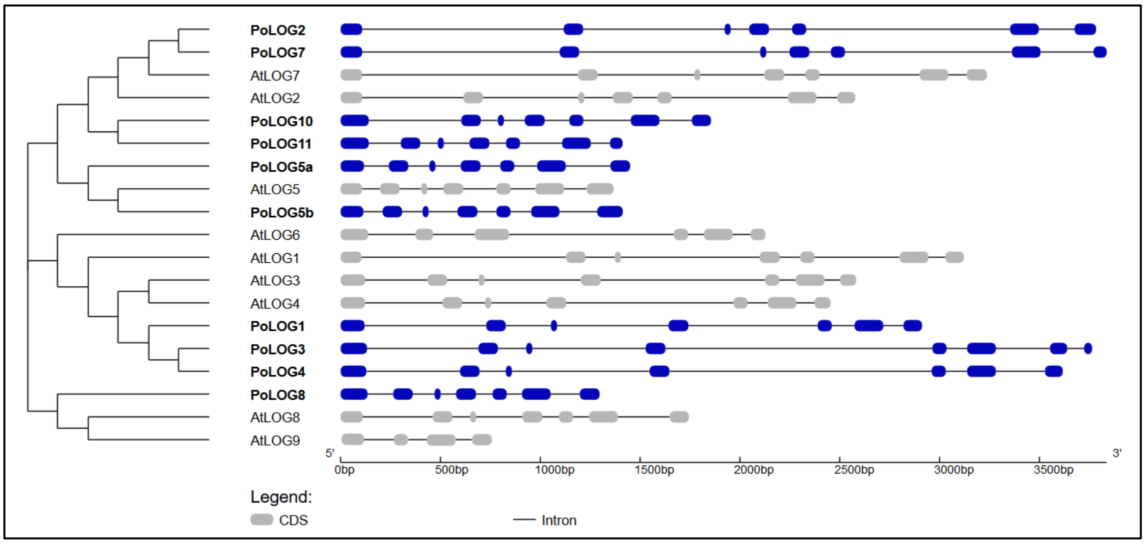
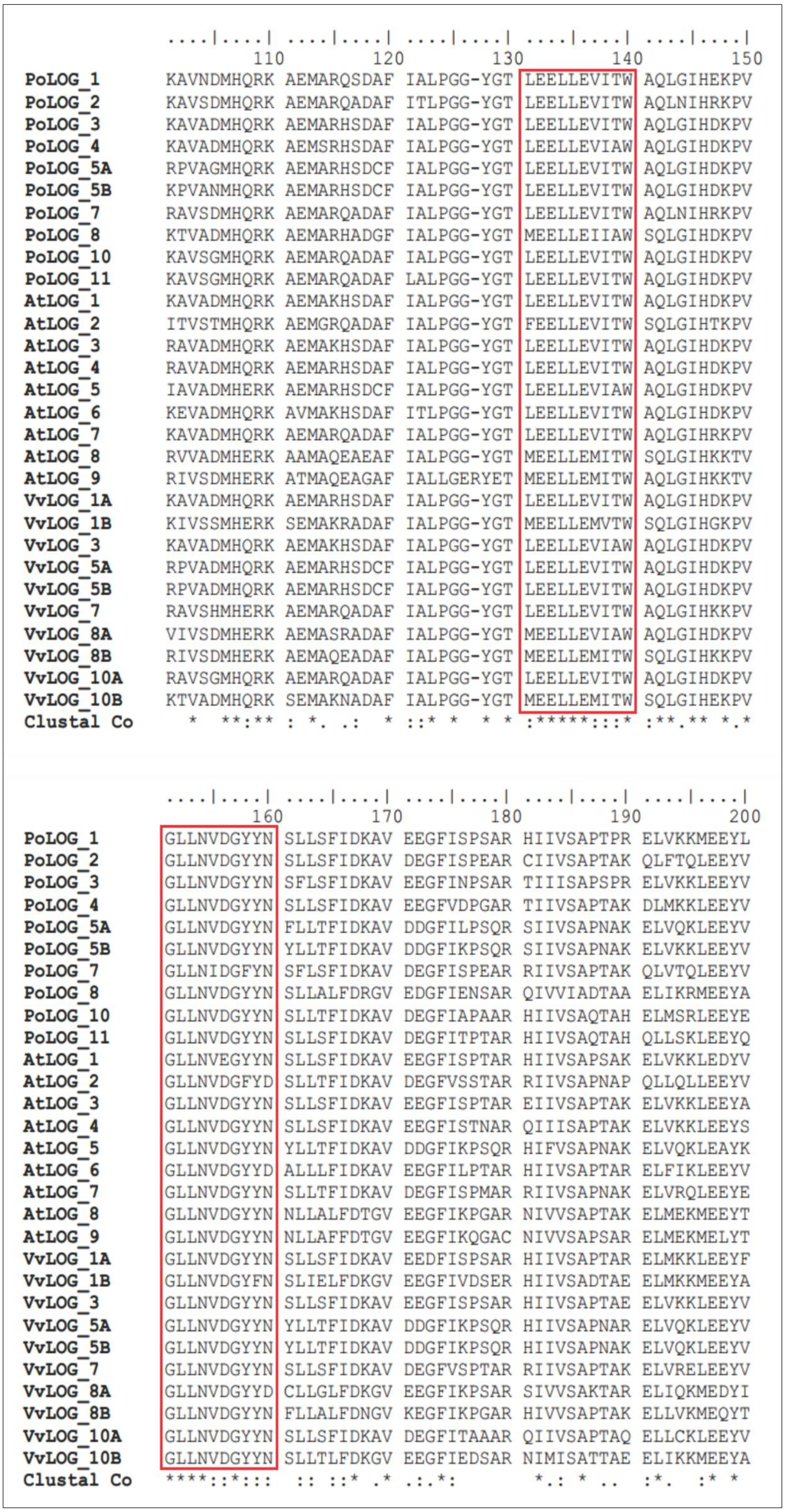


Figura 5. Estrutura dos genes da família LOG Genes em azul são de *Passiflora organensis* (Po) e em cinza de *Arabidopsis thaliana* (At).

Em *V. vinifera*, Böttcher et al. (2015) identificaram dez genes, assim como em *P. organensis* Foram identificados em *Populus trichocarpa*, 13 genes *LOG*, e em *Prunus persica* há sete (Immanen et al. 2013) enquanto *Arabidopsis thaliana* possui nove (Kuroha et al. 2009). Possivelmente, ocorreu um evento de duplicação, do gene *LOG5* em *P. organensis* (Figura 4). E isso foi observado também em outras espécies, para o mesmo gene, como em *V. vinifera* que possui também dois (*VvLOG5a* e *VvLOG5b*) (Böttcher et al. 2015) (Figura 4) e *P. trichocarpa* que possui quatro parálogos (PtLOG5a-d) (Immanen et al. 2013).

No alinhamento das proteínas da família LOG foram observadas duas regiões altamente conservadas: LEELLEVITW entre os aminoácidos 130 e 140, e GLLNVDGYYN entre os resíduos 150 e 160 (Figura 6).



```
               ....|....| ....|....| ....|....| ....|....| ....|....|
                       110        120        130        140        150
PoLOG_1        KAVNDMHQRK AEMARQSDAF IALPGG-YGT LEELLEVITW AQLGIHEKPV
PoLOG_2        KAVSDMHQRK AEMARQADAF ITLPGG-YGT LEELLEVITW AQLNIHRKPV
PoLOG_3        KAVADMHQRK AEMARHSDAF IALPGG-YGT LEELLEVITW AQLGIHDKPV
PoLOG_4        KAVADMHQRK AEMSRHSDAF IALPGG-YGT LEELLEVIAW AQLGIHDKPV
PoLOG_5A       RPVAGMHQRK AEMARHSDCF IALPGG-YGT LEELLEVITW AQLGIHDKPV
PoLOG_5B       KPVANMHQRK AEMARHSDCF IALPGG-YGT LEELLEVITW AQLGIHDKPV
PoLOG_7        RAVSDMHQRK AEMARQADAF IALPGG-YGT LEELLEVITW AQLNIHRKPV
PoLOG_8        KTVADMHQRK AEMARHADGF IALPGG-YGT MEELLEIIAW SQLGIHDKPV
PoLOG_10       KAVSGMHQRK AEMARQADAF IALPGG-YGT LEELLEVITW AQLGIHDKPV
PoLOG_11       KAVSGMHQRK AEMARQADAF LALPGG-YGT LEELLEVITW AQLGIHDKPV
AtLOG_1        KAVADMHQRK AEMAKHSDAF IALPGG-YGT LEELLEVITW AQLGIHDKPV
AtLOG_2        ITVSTMHQRK AEMGRQADAF IALPGG-YGT FEELLEVITW SQLGIHTKPV
AtLOG_3        RAVADMHQRK AEMAKHSDAF IALPGG-YGT LEELLEVITW AQLGIHDKPV
AtLOG_4        RAVADMHQRK AEMARHSDAF IALPGG-YGT LEELLEVITW AQLGIHDKPV
AtLOG_5        IAVADMHERK AEMARHSDCF IALPGG-YGT LEELLEVIAW AQLGIHDKPV
AtLOG_6        KEVADMHQRK AVMAKHSDAF ITLPGG-YGT LEELLEVITW AQLGIHDKPV
AtLOG_7        KAVADMHQRK AEMARQADAF IALPGG-YGT LEELLEVITW AQLGIHRKPV
AtLOG_8        RVVADMHERK AAMAQEAEAF IALPGG-YGT MEELLEMITW SQLGIHKKTV
AtLOG_9        RIVSDMHERK ATMAQEAGAF IALLGERYET MEELLEMITW AQLGIHKKTV
VvLOG_1A       KAVADMHQRK AEMARHSDAF IALPGG-YGT LEELLEVITW AQLGIHDKPV
VvLOG_1B       KIVSSMHERK SEMAKRADAF IALPGG-YGT MEELLEMVTW SQLGIHGKPV
VvLOG_3        KAVADMHQRK AEMAKHSDAF IALPGG-YGT LEELLEVIAW AQLGIHDKPV
VvLOG_5A       RPVADMHQRK AEMARHSDCF IALPGG-YGT LEELLEVITW AQLGIHDKPV
VvLOG_5B       RPVADMHQRK AEMARHSDCF IALPGG-YGT LEELLEVITW AQLGIHDKPV
VvLOG_7        RAVSHMHERK AEMARQADAF IALPGG-YGT LEELLEVITW AQLGIHKKPV
VvLOG_8A       VIVSDMHERK AEMASRADAF IALPGG-YGT MEELLEVIAW AQLGIHDKPV
VvLOG_8B       RIVSDMHERK AEMAQEADAF IALPGG-YGT MEELLEMITW SQLGIHKKPV
VvLOG_10A      RAVSGMHQRK AEMARQADAF IALPGG-YGT LEELLEVITW AQLGIHDKPV
VvLOG_10B      KTVADMHQRK SEMAKNADAF IALPGG-YGT MEELLEMITW SQLGIHEKPV
Clustal Co       *  **:** : *. .:  * ::* *  * * :*****:::* :**.** *.*


               ....|....| ....|....| ....|....| ....|....| ....|....|
                       160        170        180        190        200
PoLOG_1        GLLNVDGYYN SLLSFIDKAV EEGFISPSAR HIIVSAPTPR ELVKKMEEYL
PoLOG_2        GLLNVDGYYN SLLSFIDKAV DEGFISPEAR CIIVSAPTAK QLFTQLEEYV
PoLOG_3        GLLNVDGYYN SFLSFIDKAV EEGFINPSAR TIIISAPSPR ELVKKLEEYV
PoLOG_4        GLLNVDGYYN SLLSFIDKAV EEGFVDPGAR TIIVSAPTAK DLMKKLEEYV
PoLOG_5A       GLLNVDGYYN FLLTFIDKAV DDGFILPSQR SIIVSAPNAK ELVQKLEEYV
PoLOG_5B       GLLNVDGYYN YLLTFIDKAV DDGFIKPSQR SIIVSAPNAK ELVKKLEEYV
PoLOG_7        GLLNIDGFYN SFLSFIDKAV DEGFISPEAR RIIVSAPTAK QLVTQLEEYV
PoLOG_8        GLLNVDGYYN SLLALFDRGV EDGFIENSAR QIVVIADTAA ELIKRMEEYA
PoLOG_10       GLLNVDGYYN SLLTFIDKAV DEGFIAPAAR HIIVSAQTAH ELMSRLEEYE
PoLOG_11       GLLNVDGYYN SLLSFIDKAV DEGFITPTAR HIIVSAQTAH QLLSKLEEYQ
AtLOG_1        GLLNVEGYYN SLLSFIDKAV EEGFISPTAR HIIVSAPSAK ELVKKLEDYV
AtLOG_2        GLLNVDGFYD SLLTFIDKAV DEGFVSSTAR RIIVSAPNAP QLLQLLEEYV
AtLOG_3        GLLNVDGYYN SLLSFIDKAV EEGFISPTAR EIIVSAPTAK ELVKKLEEYA
AtLOG_4        GLLNVDGYYN SLLSFIDKAV EEGFISTNAR QIIISAPTAK ELVKKLEEYS
AtLOG_5        GLLNVDGYYN YLLTFIDKAV DDGFIKPSQR HIFVSAPNAK ELVQKLEAYK
AtLOG_6        GLLNVDGYYD ALLLFIDKAV EEGFILPTAR HIIVSAPTAR ELFIKLEEYV
AtLOG_7        GLLNVDGYYN SLLTFIDKAV DEGFISPMAR RIIVSAPNAK ELVRQLEEYE
AtLOG_8        GLLNVDGYYN NLLALFDTGV EEGFIKPGAR NIVVSAPTAK ELMEKMEEYT
AtLOG_9        GLLNVDGYYN NLLAFFDTGV EEGFIKQGAC NIVVSAPSAR ELMEKMELYT
VvLOG_1A       GLLNVDGYYN SLLSFIDKAV EEDFISPSAR HIIVSAPTAR ELMKKLEEYF
VvLOG_1B       GLLNVDGYFN SLIELFDKGV EEGFIVDSER HIIVSADTAE ELMKKMEEYA
VvLOG_3        GLLNVDGYYN SLLSFIDKAV EEGFISPSAR HIIVSAPTAE ELVKKLEEYV
VvLOG_5A       GLLNVDGYYN YLLTFIDKAV DDGFIKPSQR HIIVSAPNAR ELVQKLEEYV
VvLOG_5B       GLLNVDGYYN YLLTFIDKAV DDGFIKPSQR HIIVSAPNAK ELVQKLEEYV
VvLOG_7        GLLNVDGYYN SLLSFIDKAV DEGFVSPTAR RIIVSAPTAK ELVRELEEYV
VvLOG_8A       GLLNVDGYYD CLLGLFDKGV EEGFIKPSAR SIVVSAKTAR ELIQKMEDYI
VvLOG_8B       GLLNVDGYYN FLLALFDNGV KEGFIKPGAR HIVVSAPTAK ELLVKMEQYT
VvLOG_10A      GLLNVDGYYN SLLSFIDKAV DEGFITAAAR QIIVSAPTAQ ELLCKLEEYV
VvLOG_10B      GLLNVDGYYN SLLTLFDKGV EEGFIEDSAR NIMISATTAE ELIKKMEEYA
Clustal Co     ****::*:::  :: ::* .* .:.*:       *.: * ..  :*.  :* *
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Figura 6. Alinhamentos de regiões das sequências proteicas dos PoLOGs, de *Passiflora organensis*, com os AtLOGs, de *Arabidopsis thaliana* e os VvLOGs, de *Vitis vinifera* A linha Clustal Co mostra o grau de conservação entre as sequências, sendo representados por [*] os aminoácidos totalmente conservados, [:] altamente conservados e a ausência de símbolos indica que não há conservação entre os resíduos.

Família gênica *CYTOKININ OXIDASE/DEHYDROGENASES* (*CKX*)

A família gênica *CYTOKININ OXIDASE/DEHYDROGENASES* (*CKX*) codifica as enzimas que catabolizam as citocininas (Werner et al. 2001). Em *P. organensis*, foram identificados nove *CKX*, distribuídos em quatro clados (Figura 7). Estes genes apresentaram estrutura gênica mais diversa, tendo de quatro a seis éxons (Figura 8), assim como observado em outras espécies (Tan et al. 2018; Liu et al. 2013; Immanen et al. 2013). Como *A. thaliana* possui sete *CKX* (Schmülling et al. 2003), podemos considerar que em *P. organensis* houve duas duplicações, nos genes *PoCKX1a-b* e *PoCKX7a-b* (Figura 7). Em *V. vinifera* foram identificados oito genes, mas nessa espécie há três ortólogos do *AtCKX3* (*VvCKX3a-c*) (Böttcher et al. 2015) (Figura 7).

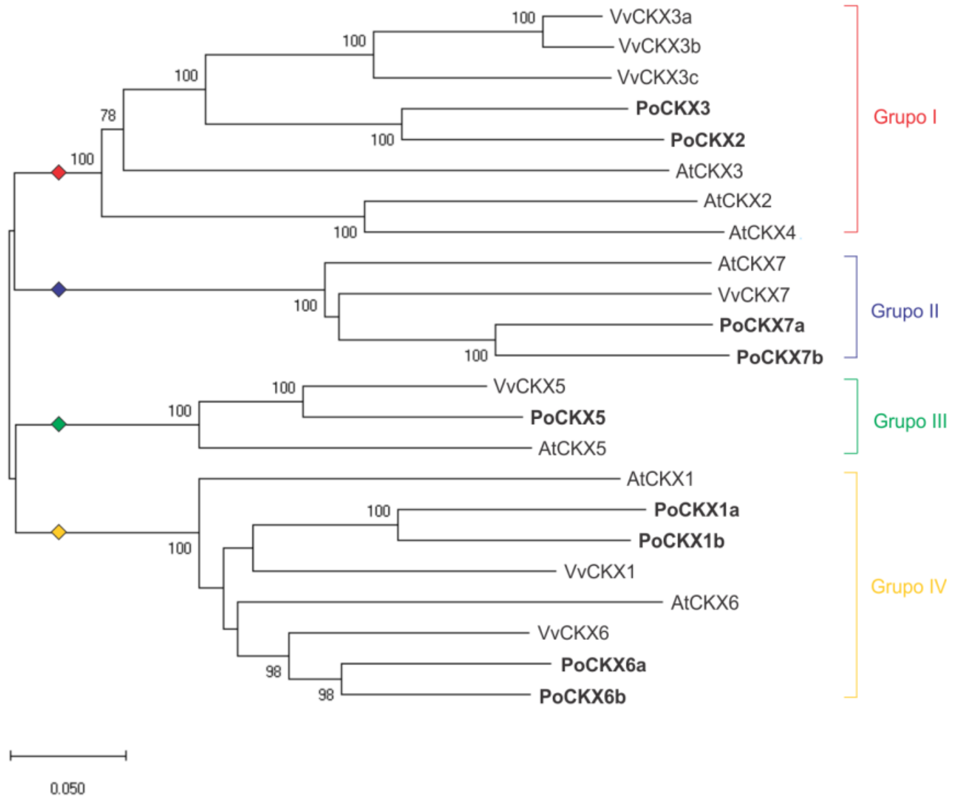


Figura 7. Árvore filogenética da família gênica *CKX* envolvida na degradação de citocinina. A árvore contém membros de *Passiflora organensis* (Po) e os ortólogos de *Arabidopsis thaliana* (At) e *Vitis vinifera* (Vv).

Em outras espécies há uma variação quanto ao número e a estrutura dos *CKX*, como em *P. trichocarpa* que contém oito ortólogos e *P. persica* que possui seis (Immanen et al. 2013) mostrando que nessa família há eventos de deleção e duplicação com frequência.

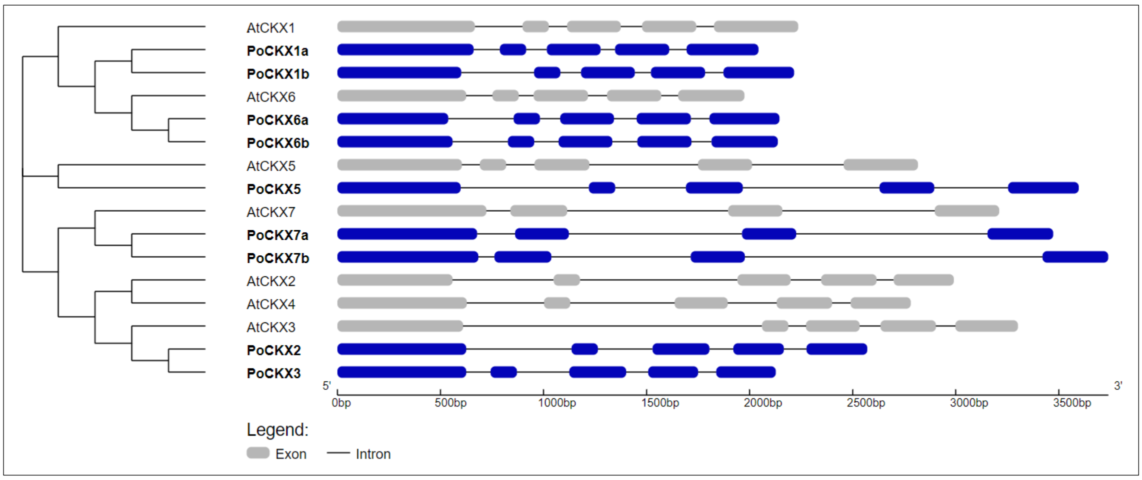
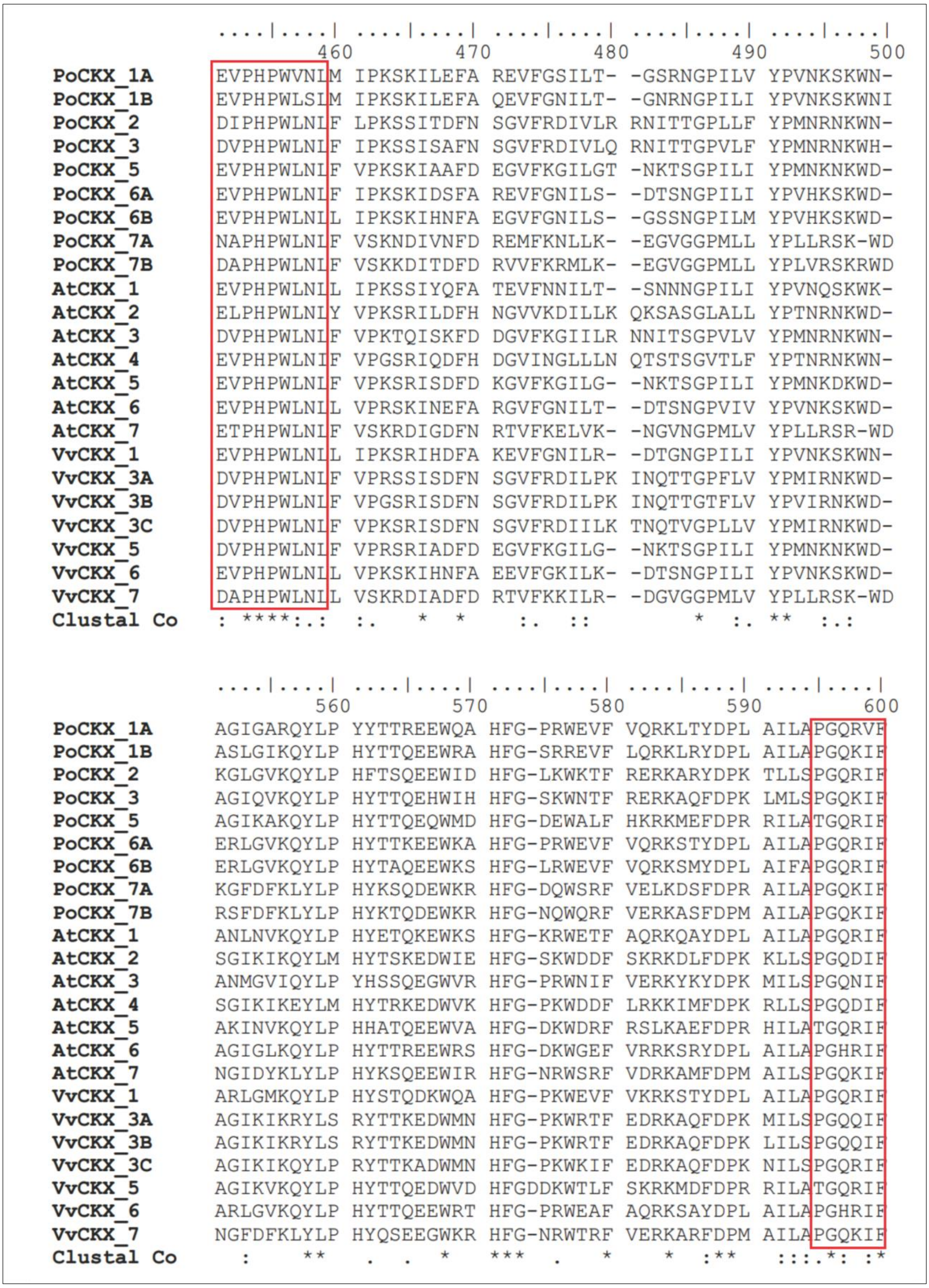


Figura 8. Estrutura dos genes da família CKX Genes em azul são de *Passiflora organensis* (Po) e em cinza de *Arabidopsis thaliana* (At).

Nas proteínas CKXs foram observadas duas regiões altamente conservadas e similares às encontradas em outras espécies: PHPWLN, entre os resíduos 450 e 460 e PGQ-IF entre as posições 590 e 600 (Figura 9).

Em uma análise da estrutura proteica dos CKXs em milho, arroz, *Arabidopsis* e outras espécies, foi identificada baixa similaridade de sequencia entre as diferentes proteínas CKX, embora cerca de um terço de todas as posições de aminoácidos sejam altamente conservadas (Schmülling et al. 2003).



```
                 ....|....| ....|....| ....|....| ....|....| ....|....|
                        460        470        480        490        500
PoCKX_1A         EVPHPWVNLM IPKSKILEFA REVFGSILT- -GSRNGPILV YPVNKSKWN-
PoCKX_1B         EVPHPWLSIM IPKSKILEFA QEVFGNILT- -GNRNGPILI YPVNKSKWNI
PoCKX_2          DIPHPWLNLF LPKSSITDFN SGVFRDIVLR RNITTGPLLF YPMNRNKWN-
PoCKX_3          DVPHPWLNLF IPKSSISAFN SGVFRDIVLQ RNITTGPVLF YPMNRNKWH-
PoCKX_5          EVPHPWLNLF VPKSKIAAFD EGVFKGILGT -NKTSGPILI YPMNKNKWD-
PoCKX_6A         EVPHPWLNLF IPKSKIDSFA REVFGNILS- -DTSNGPILI YPVHKSKWD-
PoCKX_6B         EVPHPWLNLL IPKSKIHNFA EGVFGNILS- -GSSNGPILM YPVHKSKWD-
PoCKX_7A         NAPHPWLNLF VSKNDIVNFD REMFKNLLK- -EGVGGPMLL YPLLRSK-WD
PoCKX_7B         DAPHPWLNLF VSKKDITDFD RVVFKRMLK- -EGVGGPMLL YPLVRSKRWD
AtCKX_1          EVPHPWLNLL IPKSSIYQFA TEVFNNILT- -SNNNGPILI YPVNQSKWK-
AtCKX_2          ELPHPWLNLY VPKSRILDFH NGVVKDILLK QKSASGLALL YPTNRNKWD-
AtCKX_3          DVPHPWLNLF VPKTQISKFD DGVFKGIILR NNITSGPVLV YPMNRNKWN-
AtCKX_4          EVPHPWLNIF VPGSRIQDFH DGVINGLLLN QTSTSGVTLF YPTNRNKWN-
AtCKX_5          EVPHPWLNLF VPKSRISDFD KGVFKGILG- -NKTSGPILI YPMNKDKWD-
AtCKX_6          EVPHPWLNLL VPRSKINEFA RGVFGNILT- -DTSNGPVIV YPVNKSKWD-
AtCKX_7          ETPHPWLNLF VSKRDIGDFN RTVFKELVK- -NGVNGPMLV YPLLRSR-WD
VvCKX_1          EVPHPWLNLL IPKSRIHDFA KEVFGNILR- -DTGNGPILI YPVNKSKWN-
VvCKX_3A         DVPHPWLNLF VPRSSISDFN SGVFRDILPK INQTTGPFLV YPMIRNKWD-
VvCKX_3B         DVPHPWLNLF VPGSRISDFN SGVFRDILPK INQTTGTFLV YPVIRNKWD-
VvCKX_3C         DVPHPWLNLF VPKSRISDFN SGVFRDIILK TNQTVGPLLV YPMIRNKWD-
VvCKX_5          DVPHPWLNLF VPRSRIADFD EGVFKGILG- -NKTSGPILI YPMNKNKWD-
VvCKX_6          EVPHPWLNLL VPKSKIHNFA EEVFGKILK- -DTSNGPILI YPVNKSKWD-
VvCKX_7          DAPHPWLNLL VSKRDIADFD RTVFKKILR- -DGVGGPMLV YPLLRSK-WD
Clustal Co       : ****:.:  :.   *  *    :.  ::       *  :. **  :.:


                 ....|....| ....|....| ....|....| ....|....| ....|....|
                        560        570        580        590        600
PoCKX_1A         AGIGARQYLP YYTTREEWQA HFG-PRWEVF VQRKLTYDPL AILAPGQRVF
PoCKX_1B         ASLGIKQYLP HYTTQEEWRA HFG-SRREVF LQRKLRYDPL AILAPGQKIF
PoCKX_2          KGLGVKQYLP HFTSQEEWID HFG-LKWKTF RERKARYDPK TLLSPGQRIF
PoCKX_3          AGIQVKQYLP HYTTQEHWIH HFG-SKWNTF RERKAQFDPK LMLSPGQKIF
PoCKX_5          AGIKAKQYLP HYTTQEQWMD HFG-DEWALF HKRKMEFDPR RILATGQRIF
PoCKX_6A         ERLGVKQYLP HYTTKEEWKA HFG-PRWEVF VQRKSTYDPL AILAPGQRIF
PoCKX_6B         ERLGVKQYLP HYTAQEEWKS HFG-LRWEVF VQRKSMYDPL AIFAPGQRIF
PoCKX_7A         KGFDFKLYLP HYKSQDEWKR HFG-DQWSRF VELKDSFDPR AILAPGQKIF
PoCKX_7B         RSFDFKLYLP HYKTQDEWKR HFG-NQWQRF VERKASFDPM AILAPGQKIF
AtCKX_1          ANLNVKQYLP HYETQKEWKS HFG-KRWETF AQRKQAYDPL AILAPGQRIF
AtCKX_2          SGIKIKQYLM HYTSKEDWIE HFG-SKWDDF SKRKDLFDPK KLLSPGQDIF
AtCKX_3          ANMGVIQYLP YHSSQEGWVR HFG-PRWNIF VERKYKYDPK MILSPGQNIF
AtCKX_4          SGIKIKEYLM HYTRKEDWVK HFG-PKWDDF LRKKIMFDPK RLLSPGQDIF
AtCKX_5          AKINVKQYLP HHATQEEWVA HFG-DKWDRF RSLKAEFDPR HILATGQRIF
AtCKX_6          AGIGLKQYLP HYTTREEWRS HFG-DKWGEF VRRKSRYDPL AILAPGHRIF
AtCKX_7          NGIDYKLYLP HYKSQEEWIR HFG-NRWSRF VDRKAMFDPM AILSPGQKIF
VvCKX_1          ARLGMKQYLP HYSTQDKWQA HFG-PKWEVF VKRKSTYDPL AILAPGQRIF
VvCKX_3A         AGIKIKRYLS RYTTKEDWMN HFG-PKWRTF EDRKAQFDPK MILSPGQQIF
VvCKX_3B         AGIKIKRYLS RYTTKEDWMN HFG-PKWRTF EDRKAQFDPK LILSPGQQIF
VvCKX_3C         AGIKIKQYLP RYTTKADWMN HFG-PKWKIF EDRKAQFDPK NILSPGQRIF
VvCKX_5          AGIKVKQYLP HYTTQEDWVD HFGDDKWTLF SKRKMDFDPR RILATGQRIF
VvCKX_6          ARLGVKQYLP HYTTQEEWRT HFG-PRWEAF AQRKSAYDPL AILAPGHRIF
VvCKX_7          NGFDFKLYLP HYQSEEGWKR HFG-NRWTRF VERKARFDPM AILAPGQKIF
Clustal Co         :    **   .  .  *   ***  .   *    *  :**   :::.*: :*
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Figura 9 Alinhamentos de regiões das sequências proteicas codificadas pelos genes PoCKX, de *Passiflora organensis*, com os AtCKX, de *Arabidopsis thaliana* e os VvCKX, de *Vitis vinifera*. A linha Clustal Co mostra o grau de conservação entre as sequências, sendo representados por [*] os aminoácidos totalmente conservados, [:] altamente conservados e a ausência de símbolos indica que não há conservação entre os resíduos

Famílias gênicas *RESPONSE REGULATORs* (*RRs* do tipo A e do tipo B)

Os genes que respondem à citocinina são os *RESPONSE REGULATORs*, que por terem sido inicialmente identificados em *Arabidopsis*, foram denominados *ARABIDOPSIS RESPONSE REGULATORs (ARRs*), sendo duas classes: *ARRs* do tipo A e do tipo B. Os *ARRs* do tipo B codificam fatores de transcrição com um domínio de ligação ao DNA C-terminal e um domínio receptor N-terminal, enquanto os fatores do tipo A possuem um receptor N-terminal, mas não um domínio de ligação ao DNA (Xie et al. 2018). Os reguladores de resposta do tipo B respondem positivamente à citocinina, transcrevendo os genes alvo, entre eles os *ARRs* do tipo A. Os *ARRs* do tipo A, por sua vez, podem regular negativamente a resposta a citocinina primária por meio de um *feedback* negativo, reprimindo a ação dos *ARRs* do tipo B (Heyl et al. 2003).

No presente estudo, identificamos em *P. organensis*, dez *RRs* do tipo A (*PoRR3, PoRR4, PoRR5, PoRR6, PoRR8, PoRR9, PoRR16a, PoRR16b, PoRR17a* e *PoRR17b*), e 11 *RRs* do tipo B (*PoRR1, PoRR2, PoRR10, PoRR11a, PoRR11b, PoRR12, PoRR13, PoRR14, PoRR18a, PoRR18b* e *PoRR21*) (Figura 10). O número de genes *RRs* identificados em *P. organensis* foi igual ao identificado previamente em *A. thaliana*, que possui também dez *ARRs* do tipo A (*ARR3, ARR4, ARR5, ARR6, ARR7, ARR8, ARR9, ARR15, ARR16* e *ARR17*) e 11 *ARRs* do tipo B (*ARR1, ARR2, ARR10, ARR11, ARR12, ARR13, ARR14, ARR18, ARR19, ARR20* e *ARR21*) (D'Agostino et al. 2000). Fernandes et al. (2009) identificaram em *Vitis vinifera*, quatro *ARRs* do tipo A e seis *ARRs* do tipo B.

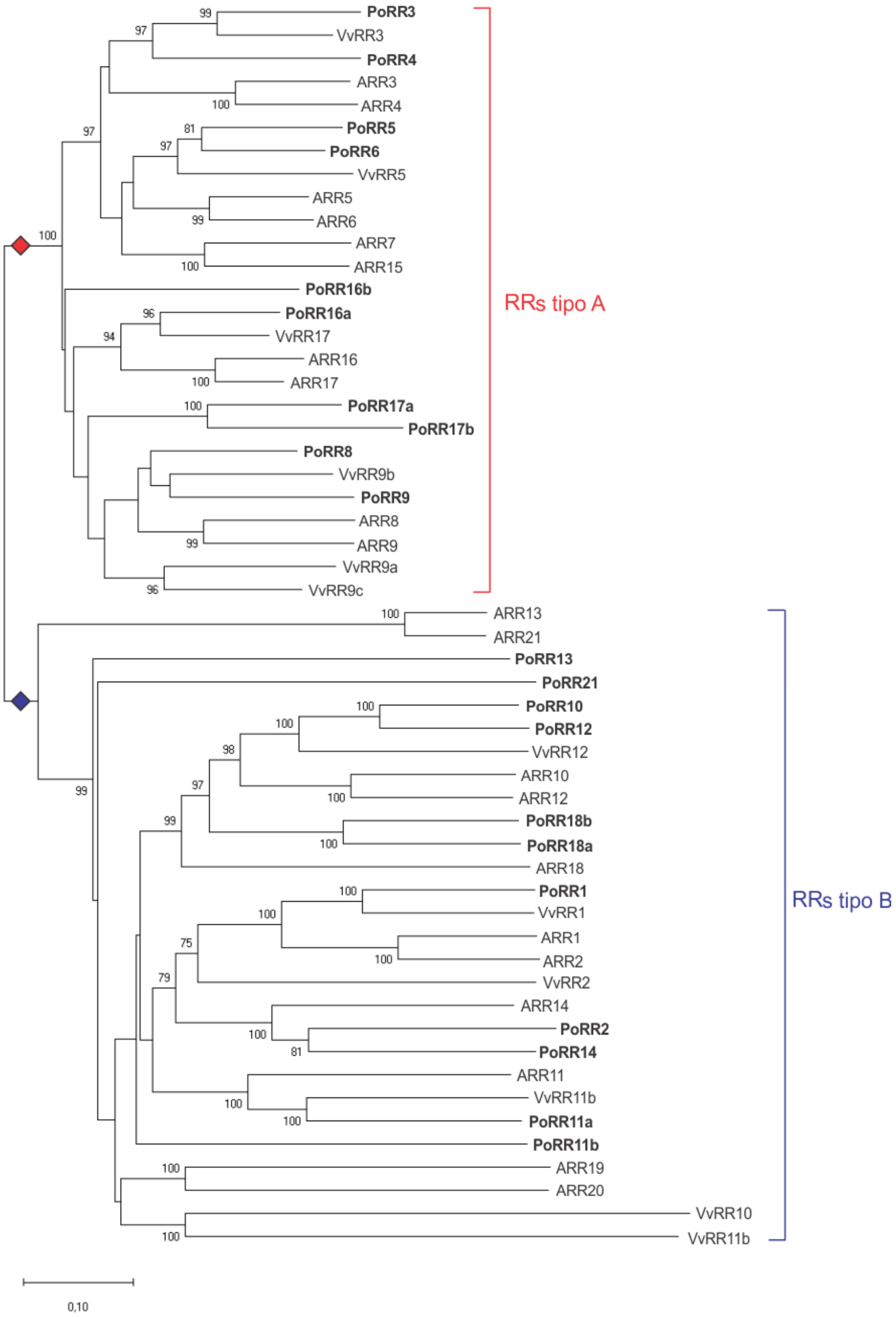


Figura 10. Árvores filogenéticas das famílias gênicas envolvidas na resposta a citocinina, contendo sequencias de *Passiflora organensis* (PoRR) e os ortólogos de *Arabidopsis thaliana* (ARR).

A estrutura gênica dos *RRs* em *P. organensis* foi similar à observada em *A. thaliana* e *V. vinifera*, tendo quatro a seis éxons nos *PoRRs* do tipo A e do tipo B

(Figura 11). Contudo, os genes da família *PoRR* do tipo A possuem tamanho menor, em torno de 1700 pb, com exceção do *PoRR17b* que apresentou em torno de 4200 pb (Figura 11). Os *PoRRs* do tipo B apresentaram de 2100 a 4800 pb (Figura 11).

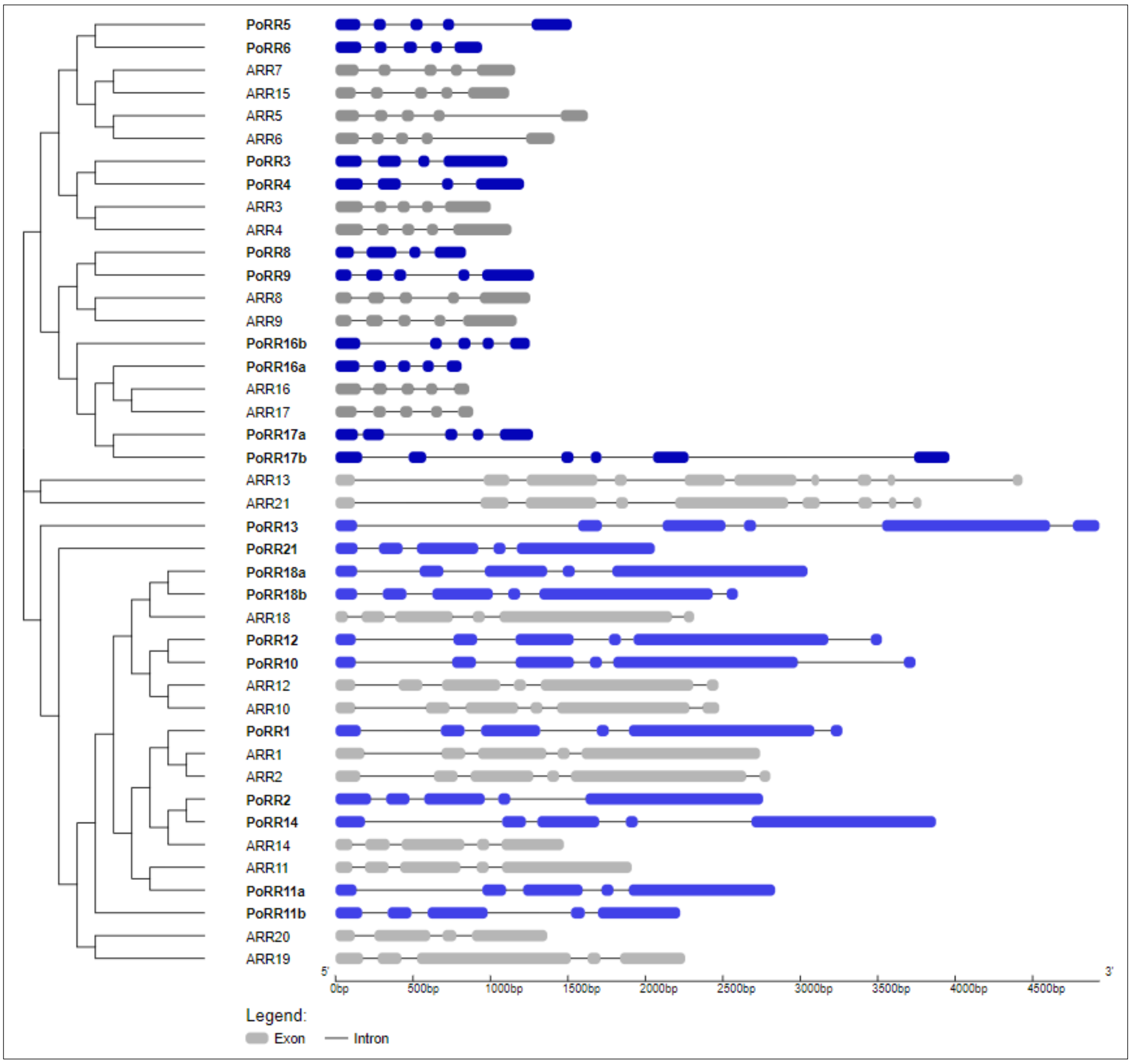
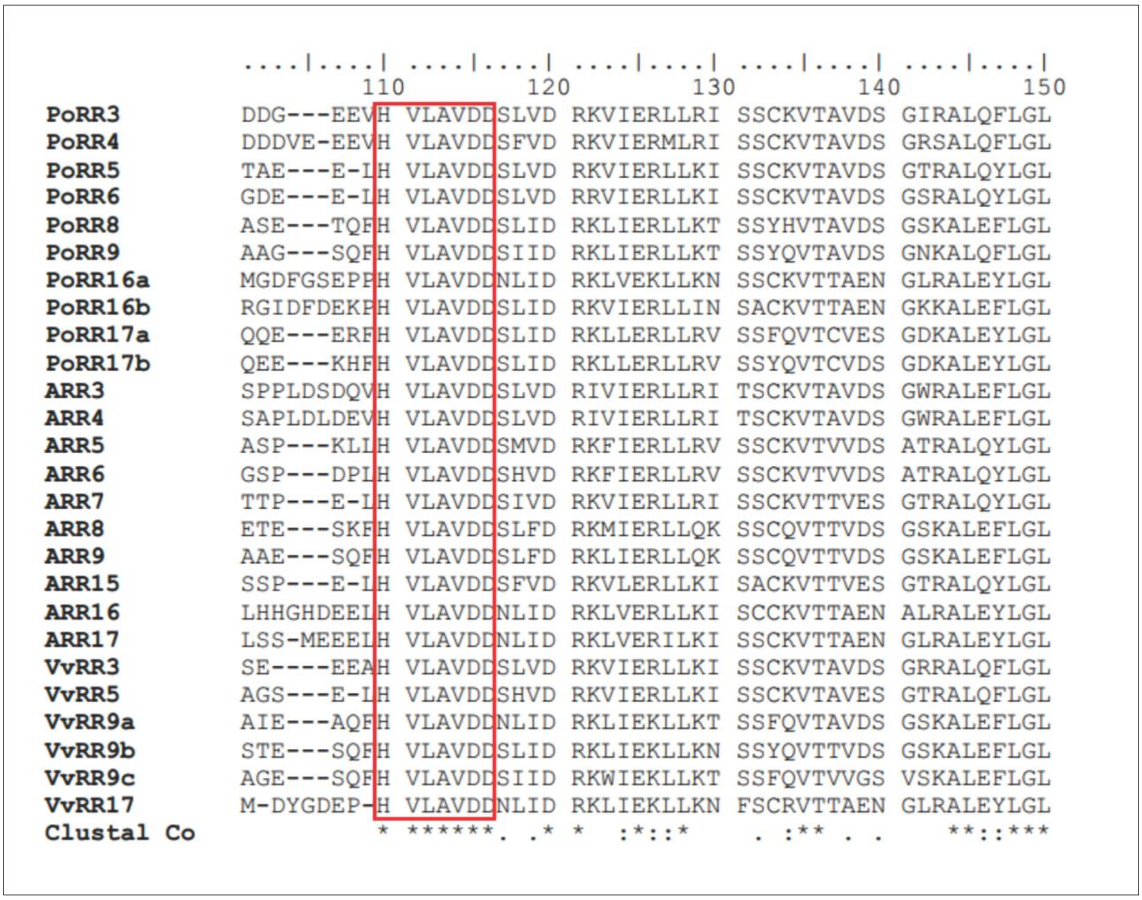


Figura 11. Estrutura dos genes da família ARR Genes em azul são de *Passiflora organensis* (Po) e em cinza de *Arabidopsis thaliana* (At).

Nas proteínas ARRs do tipo A foi observada uma região 100% conservada, contendo sete aminoácidos – HVLAVDD, localizada entre os resíduos 110 e 120 (Figura 12).



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                ....|....| ....|....| ....|....| ....|....| ....|....|
                        110        120        130        140        150
PoRR3           DDG---EEVH VLAVDDSLVD RKVIERLLRI SSCKVTAVDS GIRALQFLGL
PoRR4           DDDVE-EEVH VLAVDDSFVD RKVIERMLRI SSCKVTAVDS GRSALQFLGL
PoRR5           TAE---E-LH VLAVDDSLVD RKVIERLLKI SSCKVTAVDS GTRALQYLGL
PoRR6           GDE---E-LH VLAVDDSLVD RRVIERLLKI SSCKVTAVDS GSRALQYLGL
PoRR8           ASE---TQFH VLAVDDSLID RKLIERLLKT SSYHVTAVDS GSKALEFLGL
PoRR9           AAG---SQFH VLAVDDSIID RKLIERLLKT SSYQVTAVDS GNKALQFLGL
PoRR16a         MGDFGSEPPH VLAVDDNLID RKLVEKLLKN SSCKVTTAEN GLRALEYLGL
PoRR16b         RGIDFDEKPH VLAVDDSLID RKVIERLLIN SACKVTTAEN GKKALEFLGL
PoRR17a         QQE---ERFH VLAVDDSLID RKLLERLLRV SSFQVTCVES GDKALEYLGL
PoRR17b         QEE---KHFH VLAVDDSLID RKLLERLLRV SSYQVTCVDS GDKALEYLGL
ARR3            SPPLDSDQVH VLAVDDSLVD RIVIERLLRI TSCKVTAVDS GWRALEFLGL
ARR4            SAPLDLDEVH VLAVDDSLVD RIVIERLLRI TSCKVTAVDS GWRALEFLGL
ARR5            ASP---KLLH VLAVDDSMVD RKFIERLLRV SSCKVTVVDS ATRALQYLGL
ARR6            GSP---DPLH VLAVDDSHVD RKFIERLLRV SSCKVTVVDS ATRALQYLGL
ARR7            TTP---E-LH VLAVDDSIVD RKVIERLLRI SSCKVTTVES GTRALQYLGL
ARR8            ETE---SKFH VLAVDDSLFD RKMIERLLQK SSCQVTTVDS GSKALEFLGL
ARR9            AAE---SQFH VLAVDDSLFD RKLIERLLQK SSCQVTTVDS GSKALEFLGL
ARR15           SSP---E-LH VLAVDDSFVD RKVLERLLKI SACKVTTVES GTRALQYLGL
ARR16           LHHGHDEELH VLAVDDNLID RKLVERLLKI SCCKVTTAEN ALRALEYLGL
ARR17           LSS-MEEELH VLAVDDNLID RKLVERILKI SSCKVTTAEN GLRALEYLGL
VvRR3           SE----EEAH VLAVDDSLVD RKVIERLLKI SSCKVTAVDS GRRALQFLGL
VvRR5           AGS---E-LH VLAVDDSHVD RKVIERLLKI SSCKVTAVES GTRALQFLGL
VvRR9a          AIE---AQFH VLAVDDNLID RKLIEKLLKT SSFQVTAVDS GSKALEFLGL
VvRR9b          STE---SQFH VLAVDDSLID RKLIEKLLKN SSYQVTTVDS GSKALEFLGL
VvRR9c          AGE---SQFH VLAVDDSIID RKWIEKLLKT SSFQVTVVGS VSKALEFLGL
VvRR17          M-DYGDEP-H VLAVDDNLID RKLIEKLLKN FSCRVTTAEN GLRALEYLGL
Clustal Co               * ******. .* *  :*::*    . :** . .    **::***
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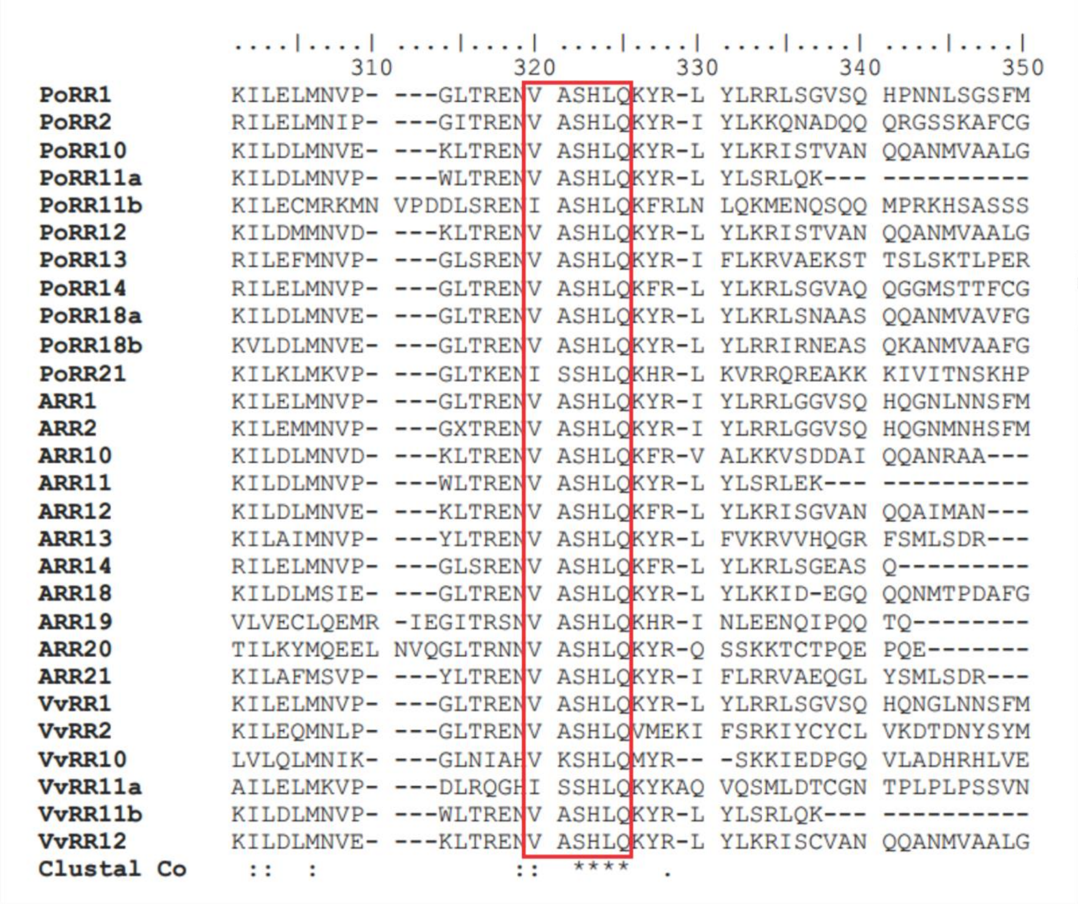
Figura 12. Alinhamentos de regiões das sequências proteicas dos RRs do tipo A, sendo PoRR, de *Passiflora organensis*, os ARR, de *Arabidopsis thaliana* e os VvRR, de *Vitis vinifera* A linha Clustal Co mostra o grau de conservação entre as sequências, sendo representados por [*] os aminoácidos totalmente conservados, [:] altamente conservados e a ausência de símbolos indica que não há conservação entre os resíduos.

Nas proteínas ARRs do tipo B, a região 100% conservada observada tinha apenas quatro aminoácidos – SHLQ – localizados entre as posições 320 e 330, e precedidos por resíduos pouco conservados (Figura 13).



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                ....|....| ....|....| ....|....| ....|....| ....|....|
                        310        320        330        340        350
PoRR1           KILELMNVP- ---GLTRENV ASHLQKYR-L YLRRLSGVSQ HPNNLSGSFM
PoRR2           RILELMNIP- ---GITRENV ASHLQKYR-I YLKKQNADQQ QRGSSKAFCG
PoRR10          KILDLMNVE- ---KLTRENV ASHLQKYR-L YLKRISTVAN QQANMVAALG
PoRR11a         KILDLMNVP- ---WLTRENV ASHLQKYR-L YLSRLQK--- ----------
PoRR11b         KILECMRKMN VPDDLSRENI ASHLQKFRLN LQKMENQSQQ MPRKHSASSS
PoRR12          KILDMMNVD- ---KLTRENV ASHLQKYR-L YLKRISTVAN QQANMVAALG
PoRR13          RILEFMNVP- ---GLSRENV ASHLQKYR-I FLKRVAEKST TSLSKTLPER
PoRR14          RILELMNVP- ---GLTRENV ASHLQKFR-L YLKRLSGVAQ QGGMSTTFCG
PoRR18a         KILDLMNVE- ---GLTRENV ASHLQKYR-L YLKRLSNAAS QQANMVAVFG
PoRR18b         KVLDLMNVE- ---GLTRENV ASHLQKYR-L YLRRIRNEAS QKANMVAAFG
PoRR21          KILKLMKVP- ---GLTKENI SSHLQKHR-L KVRRQREAKK KIVITNSKHP
ARR1            KILELMNVP- ---GLTRENV ASHLQKYR-I YLRRLGGVSQ HQGNLNNSFM
ARR2            KILEMMNVP- ---GXTRENV ASHLQKYR-I YLRRLGGVSQ HQGNMNHSFM
ARR10           KILDLMNVD- ---KLTRENV ASHLQKFR-V ALKKVSDDAI QQANRAA---
ARR11           KILDLMNVP- ---WLTRENV ASHLQKYR-L YLSRLEK--- ----------
ARR12           KILDLMNVE- ---KLTRENV ASHLQKFR-L YLKRISGVAN QQAIMAN---
ARR13           KILAIMNVP- ---YLTRENV ASHLQKYR-L FVKRVVHQGR FSMLSDR---
ARR14           RILELMNVP- ---GLSRENV ASHLQKFR-L YLKRLSGEAS Q---------
ARR18           KILDLMSIE- ---GLTRENV ASHLQKYR-L YLKKID-EGQ QQNMTPDAFG
ARR19           VLVECLQEMR -IEGITRSNV ASHLQKHR-I NLEENQIPQQ TQ--------
ARR20           TILKYMQEEL NVQGLTRNNV ASHLQKYR-Q SSKKTCTPQE PQE-------
ARR21           KILAFMSVP- ---YLTRENV ASHLQKYR-I FLRRVAEQGL YSMLSDR---
VvRR1           KILELMNVP- ---GLTRENV ASHLQKYR-L YLRRLSGVSQ HQNGLNNSFM
VvRR2           KILEQMNLP- ---GLTRENV ASHLQVMEKI FSRKIYCYCL VKDTDNYSYM
VvRR10          LVLQLMNIK- ---GLNIAHV KSHLQMYR-- -SKKIEDPGQ VLADHRHLVE
VvRR11a         AILELMKVP- ---DLRQGHI SSHLQKYKAQ VQSMLDTCGN TPLPLPSSVN
VvRR11b         KILDLMNVP- ---WLTRENV ASHLQKYR-L YLSRLQK--- ----------
VvRR12          KILDLMNVE- ---KLTRENV ASHLQKYR-L YLKRISCVAN QQANMVAALG
Clustal Co       ::  :             ::  ****  .
```

Figura 13. Alinhamentos de regiões das sequências proteicas das RRs do tipo B, sendo PoRR, de *Passiflora organensis*, ARRs, de *Arabidopsis thaliana* e VvRRs, de *Vitis vinifera* A linha Clustal Co mostra o grau de conservação entre as sequências, sendo representados por [*] os aminoácidos totalmente conservados, [:] altamente conservados e a ausência de símbolos indica que não há conservação entre os resíduos.

Filogenia e estrutura dos genes candidatos envolvidos no metabolismo e resposta à giberelina

Famílias gênicas *GA3OXIDASE (GA3ox), GA20OXIDASE (GA20ox) e GA2OXIDASE (GA2ox)*

Há duas famílias de genes envolvidas na síntese de giberelina (*GA3ox* e *GA20ox*) e uma envolvida na degradação (*GA2ox*). As proteínas codificadas pelos genes *GA2ox*, formaram claramente dois grupos: um formado pelos homólogos *PoGA2ox2, 3, 4a*, *4b*, *6a* e *6b*, e seus ortólogos em *A. thaliana* e *V. vinifera*, e outro formado por *PoGA2ox7* e *8* e seus ortólogos (Figura 14). Dos *GA3ox*, foram identificados quatro em *P. organensis* (Figura 14).

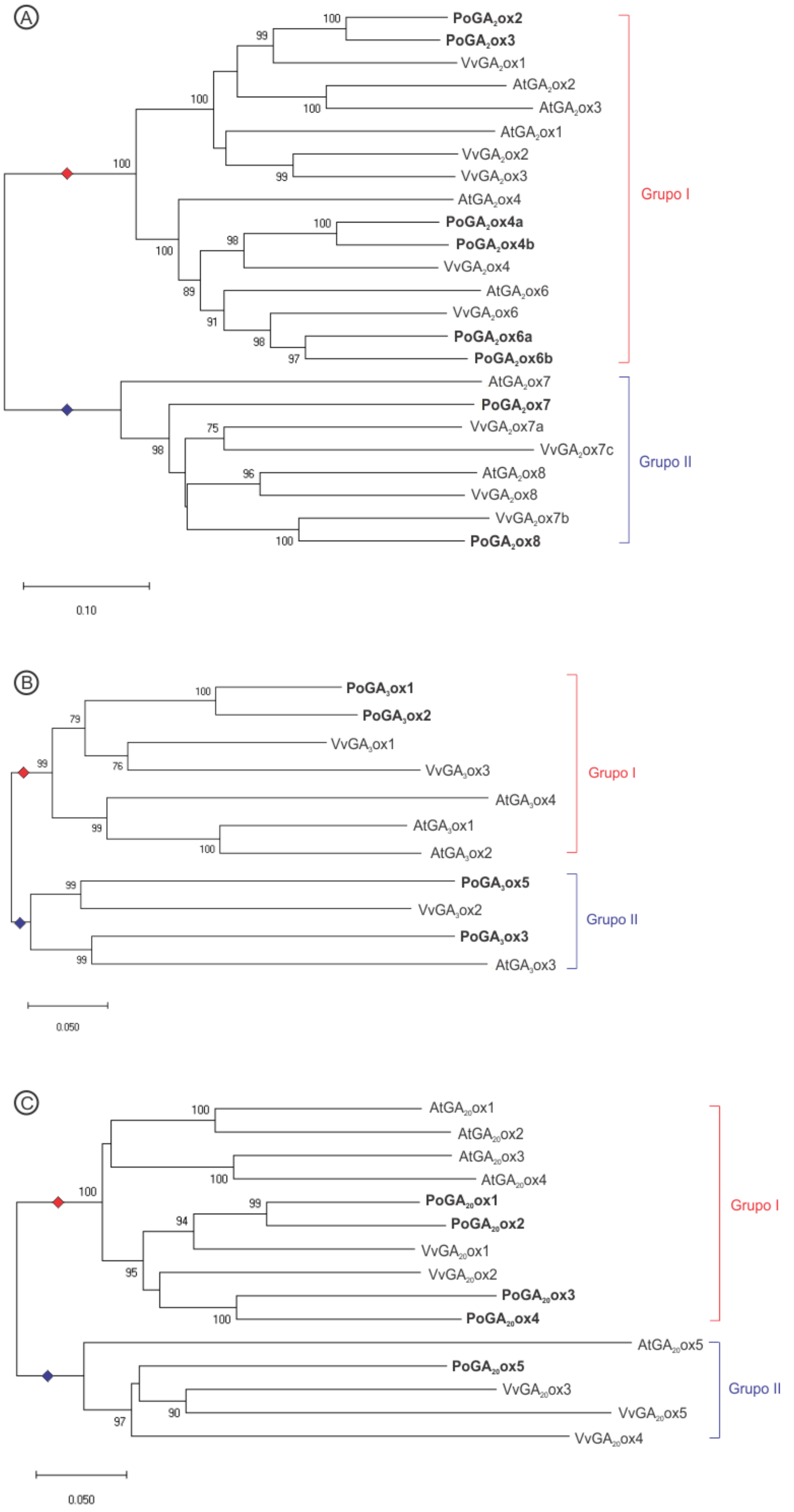


Figura 14. Árvores filogenéticas das famílias gênicas envolvidas no metabolismo de giberelina, contendo sequencias de *Passiflora organensis* (Po) e os ortólogos de *Arabidopsis thaliana* (At) e *Vitis vinifera* (Vv): (A) *GA2ox*; (B) *GA3ox*; (C) *GA20ox*.

Em *P. organensis*, as três famílias gênicas apresentam estrutura conservada, e semelhantes às estruturas dos homólogos em *A. thaliana* e *V. vinifera*. Os genes *PoGA3ox* apresentaram dois éxons, enquanto os *PoGA2ox* e *PoGA20ox* apresentaram três éxons, assim como em *A. thaliana* (Figura 15).

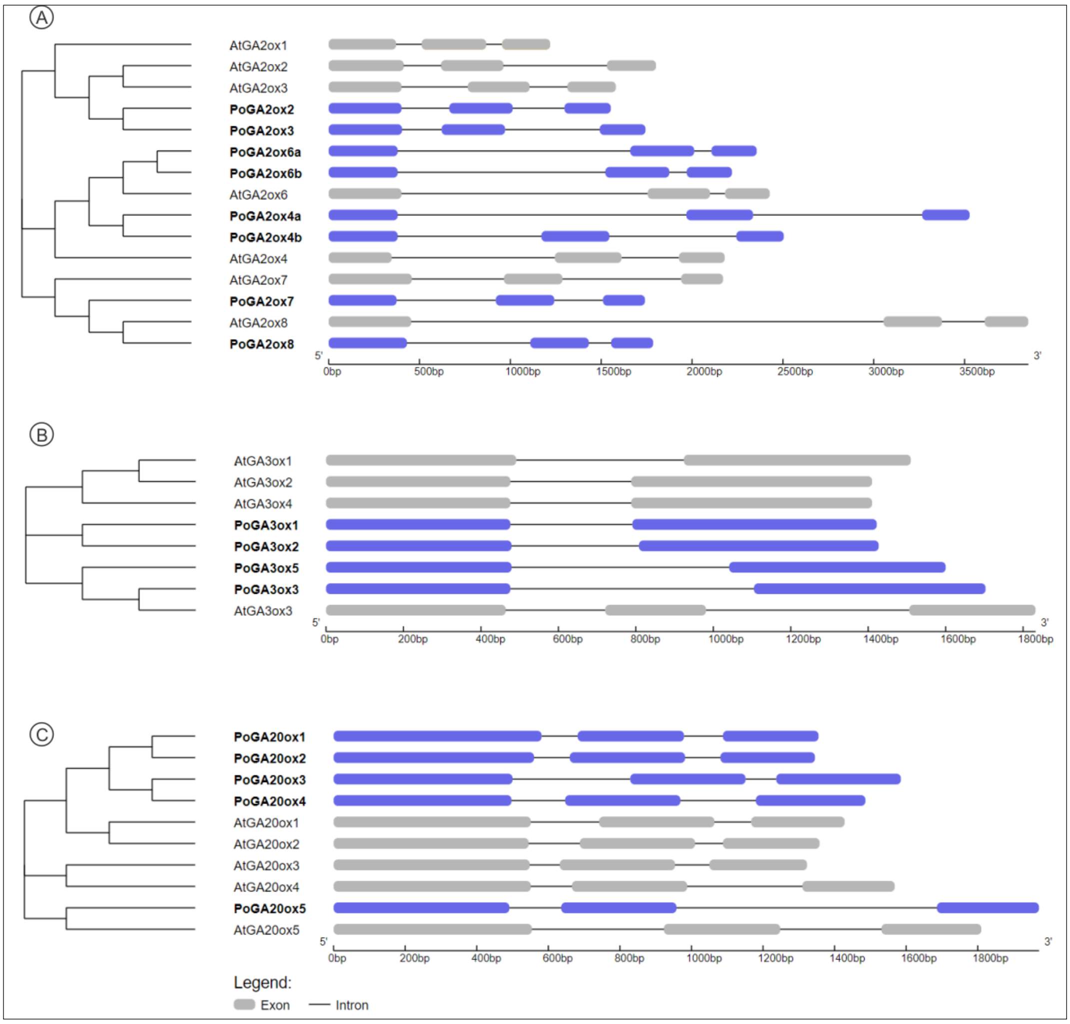


Figura 15. Estrutura dos genes das famílias *GA2ox*, *GA3ox* e *GA20ox*. Genes em azul são de *Passiflora organensis* (Po) e em cinza de *Arabidopsis thaliana* (At).

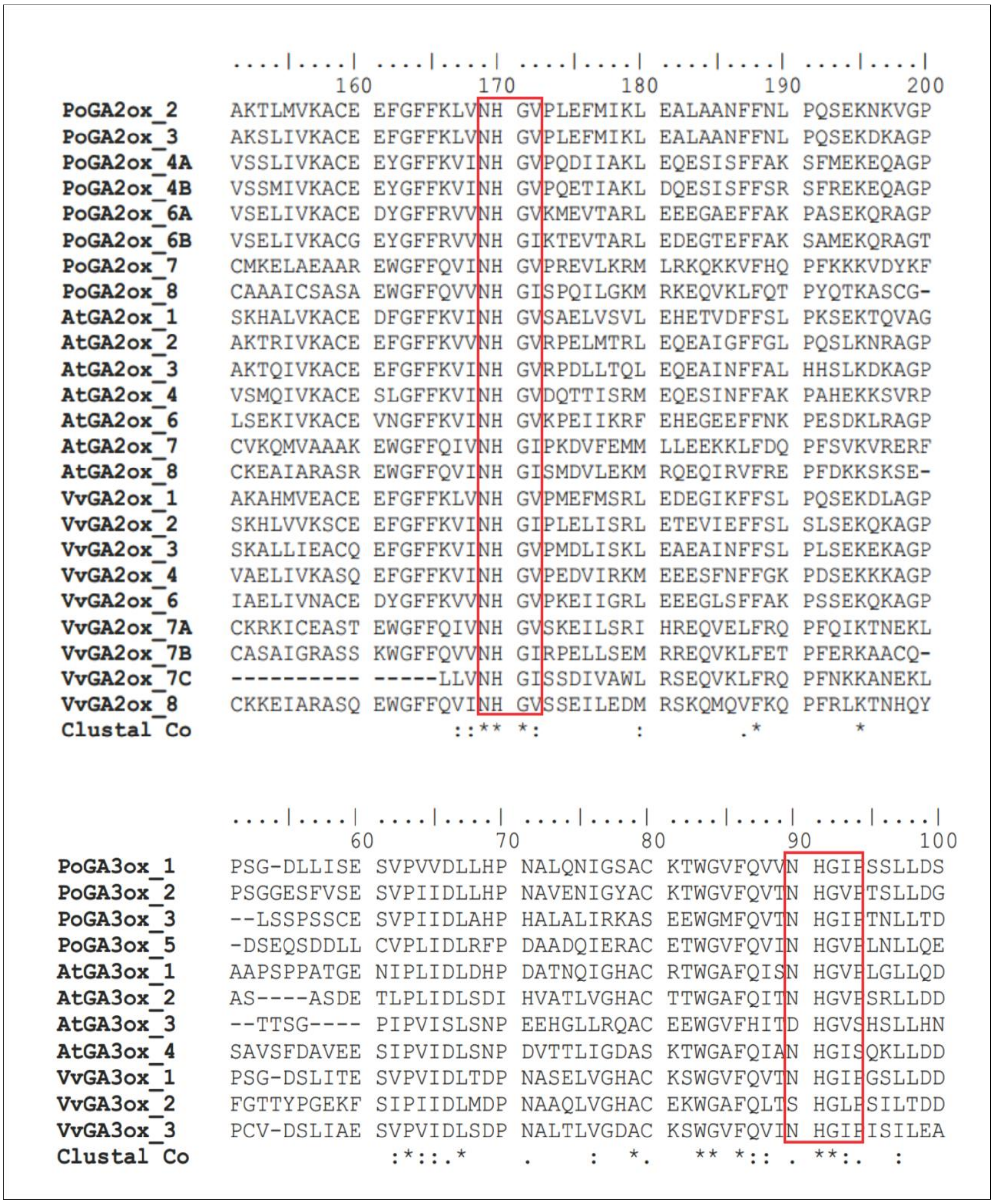
Giacomelli et al. (2013) apresentaram uma hipótese para o surgimento dos *GA oxidases*, tendo analisado *V. vinifera* em comparação com *A. thaliana*. Os autores consideraram que os *GA oxidases* teriam surgido por duplicação gênica e posterior neofuncionalização, sendo que *GA2ox* e *GA3ox* descendem de um ancestral comum.

A análise filogenética das *GA20ox* mostrou dois grupos (Figura 14C), sendo que um incluiu *PoGA20ox1*, *PoGA20ox2*, *PoGA20ox3* e *PoGA20ox4* com os ortólogos de *A. thaliana* (*AtGA20ox1*, *AtGA20ox2*, *AtGA20ox3* e *AtGA20ox4*) e apenas os

VvGA20ox1 e *VvGA20ox2* de *V. vinífera*. Outro grupo incluía *PoGA20ox5*, *AtGA20ox5* e os genes restantes de *V. vinifera*, *VvGA20ox3*, *VvGA20ox4* e *VvGA20ox5*. Uma análise anterior com *V. vinifera* e *A. thaliana* mostrou que as proteínas VvGA20ox compartilham duas sequências conservadas, sendo um resíduo LPWKET para ligação de substrato e NYYPXCXXP para a ligação de 2-oxoglutarato. Porém, as proteínas VvGA20ox1 e VvGA20ox2 não continham o resíduo LPWKET e estes formavam um clado com AtGA20ox1 e AtGA20ox2. O outro clado incluía AtGA20ox5 relacionada a VvGA20ox3, VvGA20ox4 e VvGA20ox5, que possuíam os dois resíduos (Jung et al. 2014).

As famílias gênicas GAOXIDASES têm sido estudadas em diferentes espécies vegetais e a maioria dos parálogos mostraram diferentes padrões de expressão tecidual que pode também indicar especificidade funcional (Giacomelli et al. 2013; Honi et al. 2020; Cheng et al. 2021). Em Arabidopsis, há cinco GA20ox, quatro GA3ox e sete GA2ox (Yamaguchi 2008; Rieu et al. 2008; Li et al. 2019). Para analisar as possíveis funções destes genes, foram realizados estudos com mutantes. Rieu et al. (2008) buscaram determinar os papeis fisiológicos de AtGA20ox1 e AtGA20ox2 e notaram que estes genes agem de forma redundante no controle das seguintes características: alongamento do hipocótilo e do entrenó, tempo de floração, alongamento dos filamentos da antera, número de sementes que se desenvolvem por fruto e alongamento do fruto. Contudo, mutantes duplos *atga20ox1* e *atga20ox2* não tiveram expansão foliar e crescimento das raízes afetados, indicando que os outros parálogos da mesma família contribuem para os processos de desenvolvimento examinados (Rieu et al. 2008). Em relação aos At*GA2ox*, há evidências de que estes parálogos apresentam especificidade funcional, pois todos os sete genes identificados desta família apresentam expressão diferencial nos tecidos de plantas juvenis, além de apresentarem diferentes respostas a condições de estresse (Li et al. 2019).

Nas famílias *GA2ox* e *GA3ox* houve pouca conservação das sequências em geral (Figura 16) Contudo, a região NHGv foi observada em ambas as famílias.



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               ....|....| ....|....| ....|....| ....|....| ....|....|
                      160        170        180        190        200
PoGA2ox_2      AKTLMVKACE EFGFFKLVNH GVPLEFMIKL EALAANFFNL PQSEKNKVGP
PoGA2ox_3      AKSLIVKACE EFGFFKLVNH GVPLEFMIKL EALAANFFNL PQSEKDKAGP
PoGA2ox_4A     VSSLIVKACE EYGFFKVINH GVPQDIIAKL EQESISFFAK SFMEKEQAGP
PoGA2ox_4B     VSSMIVKACE EYGFFKVINH GVPQETIAKL DQESISFFSR SFREKEQAGP
PoGA2ox_6A     VSELIVKACE DYGFFRVVNH GVKMEVTARL EEEGAEFFAK PASEKQRAGP
PoGA2ox_6B     VSELIVKACG EYGFFRVVNH GIKTEVTARL EDEGTEFFAK SAMEKQRAGT
PoGA2ox_7      CMKELAEAAR EWGFFQVINH GVPREVLKRM LRKQKKVFHQ PFKKKVDYKF
PoGA2ox_8      CAAAICSASA EWGFFQVVNH GISPQILGKM RKEQVKLFQT PYQTKASCG-
AtGA2ox_1      SKHALVKACE DFGFFKVINH GVSAELVSVL EHETVDFFSL PKSEKTQVAG
AtGA2ox_2      AKTRIVKACE EFGFFKVVNH GVRPELMTRL EQEAIGFFGL PQSLKNRAGP
AtGA2ox_3      AKTQIVKACE EFGFFKVINH GVRPDLLTQL EQEAINFFAL HHSLKDKAGP
AtGA2ox_4      VSMQIVKACE SLGFFKVINH GVDQTTISRM EQESINFFAK PAHEKKSVRP
AtGA2ox_6      LSEKIVKACE VNGFFKVINH GVKPEIIKRF EHEGEEFFNK PESDKLRAGP
AtGA2ox_7      CVKQMVAAAK EWGFFQIVNH GIPKDVFEMM LLEEKKLFDQ PFSVKVRERF
AtGA2ox_8      CKEAIARASR EWGFFQVINH GISMDVLEKM RQEQIRVFRE PFDKKSKSE-
VvGA2ox_1      AKAHMVEACE EFGFFKLVNH GVPMEFMSRL EDEGIKFFSL PQSEKDLAGP
VvGA2ox_2      SKHLVVKSCE EFGFFKVINH GIPLELISRL ETEVIEFFSL SLSEKQKAGP
VvGA2ox_3      SKALLIEACQ EFGFFKVINH GVPMDLISKL EAEAINFFSL PLSEKEKAGP
VvGA2ox_4      VAELIVKASQ EFGFFKVINH GVPEDVIRKM EEESFNFFGK PDSEKKKAGP
VvGA2ox_6      IAELIVNACE DYGFFKVVNH GVPKEIIGRL EEEGLSFFAK PSSEKQKAGP
VvGA2ox_7A     CKRKICEAST EWGFFQIVNH GVSKEILSRI HREQVELFRQ PFQIKTNEKL
VvGA2ox_7B     CASAIGRASS KWGFFQVVNH GIRPELLSEM RREQVKLFET PFERKAACQ-
VvGA2ox_7C     ---------- -----LLVNH GISSDIVAWL RSEQVKLFRQ PFNKKANEKL
VvGA2ox_8      CKKEIARASQ EWGFFQVINH GVSSEILEDM RSKQMQVFKQ PFRLKTNHQY
Clustal_Co                       ::** *:       :       .*       *

               ....|....| ....|....| ....|....| ....|....| ....|....|
                       60         70         80         90        100
PoGA3ox_1      PSG-DLLISE SVPVVDLLHP NALQNIGSAC KTWGVFQVVN HGIPSSLLDS
PoGA3ox_2      PSGGESFVSE SVPIIDLLHP NAVENIGYAC KTWGVFQVTN HGVPTSLLDG
PoGA3ox_3      --LSSPSSCE SVPIIDLAHP HALALIRKAS EEWGMFQVTN HGIPTNLLTD
PoGA3ox_5      -DSEQSDDLL CVPLIDLRFP DAADQIERAC ETWGVFQVIN HGVPLNLLQE
AtGA3ox_1      AAPSPPATGE NIPLIDLDHP DATNQIGHAC RTWGAFQISN HGVPLGLLQD
AtGA3ox_2      AS----ASDE TLPLIDLSDI HVATLVGHAC TTWGAFQITN HGVPSRLLDD
AtGA3ox_3      --TTSG---- PIPVISLSNP EEHGLLRQAC EEWGVFHITD HGVSHSLLHN
AtGA3ox_4      SAVSFDAVEE SIPVIDLSNP DVTTLIGDAS KTWGAFQIAN HGISQKLLDD
VvGA3ox_1      PSG-DSLITE SVPVIDLTDP NASELVGHAC KSWGVFQVTN HGIPGSLLDD
VvGA3ox_2      FGTTYPGEKF SIPIIDLMDP NAAQLVGHAC EKWGAFQLTS HGLPSILTDD
VvGA3ox_3      PCV-DSLIAE SVPVIDLSDP NALTLVGDAC KSWGVFQVIN HGIPISILEA
Clustal_Co                 :*::.*    .    :  *.   ** *:: . **:.  :
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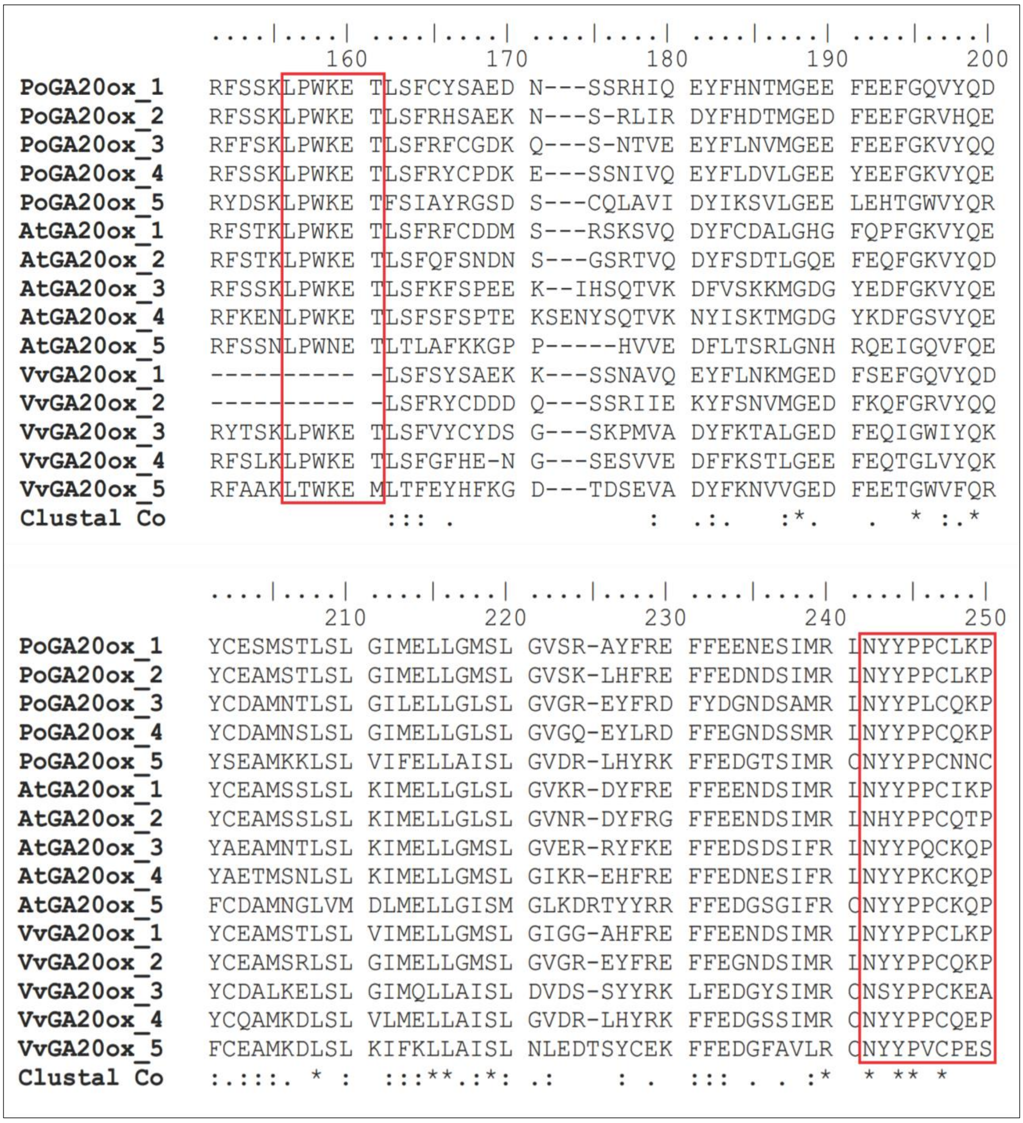
Figura 16. Alinhamentos de regiões das sequências proteicas das GA2ox e GA3ox, sendo PoGA2ox e PoGA3ox, de *Passiflora organensis*, AtGA2ox e AtGA3ox, de *Arabidopsis thaliana* e VvGA2ox e VvGA3ox, de *Vitis vinifera.* A linha Clustal Co mostra o grau de conservação entre as sequências, sendo representados por [*] os aminoácidos totalmente conservados, [:] altamente conservados e a ausência de símbolos indica que não há conservação entre os resíduos.

A família PoGA2ox apresentou poucas regiões totalmente conservadas (Figura 17), assim como as PoGA2ox e PoGA2ox. Contudo, as sequências LPWKET entre os resíduos 155 e 161, e NYYPXCXXP, entre 240 e 250, mostraram-se conservadas entre as espécies analisadas.

Em arroz (*Oryza sativa*), OsGA20ox1 apresentou maior similaridade de sequencia com o ortólogo de *Arabidopsis* AtGA20ox1 (Sakamoto et al. 2004) A sequência consenso NYYPXCXXP de ligação ao 2-oxoglutarato foi conservada em todas as proteínas OsGA20ox (Sakamoto et al. 2004) Uma sequência LPWKET, que é considerada envolvida na ligação dos substratos de GA, também foi conservado em todas as proteínas OsGA20ox (Sakamoto et al. 2004). Estas sequências consenso foram identificadas também em milho (*Zea mays*) (Song et al. 2011) e em uva (*Vitis vinifera*) (Jung et al. 2014).



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                ....|....| ....|....| ....|....| ....|....| ....|....|
                       160        170        180        190        200
PoGA20ox_1      RFSSKLPWKE TLSFCYSAED N---SSRHIQ EYFHNTMGEE FEEFGQVYQD
PoGA20ox_2      RFSSKLPWKE TLSFRHSAEK N---S-RLIR DYFHDTMGED FEEFGRVHQE
PoGA20ox_3      RFFSKLPWKE TLSFRFCGDK Q---S-NTVE EYFLNVMGEE FEEFGKVYQQ
PoGA20ox_4      RFSSKLPWKE TLSFRYCPDK E---SSNIVQ EYFLDVLGEE YEEFGKVYQE
PoGA20ox_5      RYDSKLPWKE TFSIAYRGSD S---CQLAVI DYIKSVLGEE LEHTGWVYQR
AtGA20ox_1      RFSTKLPWKE TLSFRFCDDM S---RSKSVQ DYFCDALGHG FQPFGKVYQE
AtGA20ox_2      RFSTKLPWKE TLSFQFSNDN S---GSRTVQ DYFSDTLGQE FEQFGKVYQD
AtGA20ox_3      RFSSKLPWKE TLSFKFSPEE K--IHSQTVK DFVSKKMGDG YEDFGKVYQE
AtGA20ox_4      RFKENLPWKE TLSFSFSPTE KSENYSQTVK NYISKTMGDG YKDFGSVYQE
AtGA20ox_5      RFSSNLPWNE TLTLAFKKGP P-----HVVE DFLTSRLGNH RQEIGQVFQE
VvGA20ox_1      ---------- -LSFSYSAEK K---SSNAVQ EYFLNKMGED FSEFGQVYQD
VvGA20ox_2      ---------- -LSFRYCDDD Q---SSRIIE KYFSNVMGED FKQFGRVYQQ
VvGA20ox_3      RYTSKLPWKE TLSFVYCYDS G---SKPMVA DYFKTALGED FEQIGWIYQK
VvGA20ox_4      RFSLKLPWKE TLSFGFHE-N G---SESVVE DFFKSTLGEE FEQTGLVYQK
VvGA20ox_5      RFAAKLTWKE MLTFEYHFKG D---TDSEVA DYFKNVVGED FEETGWVFQR
Clustal Co                  ::: .             :  .:.   :*.   .  * :.*

                ....|....| ....|....| ....|....| ....|....| ....|....|
                       210        220        230        240        250
PoGA20ox_1      YCESMSTLSL GIMELLGMSL GVSR-AYFRE FFEENESIMR INYYPPCLKP
PoGA20ox_2      YCEAMSTLSL GIMELLGMSL GVSK-LHFRE FFEDNDSIMR INYYPPCLKP
PoGA20ox_3      YCDAMNTLSL GILELLGLSL GVGR-EYFRD FYDGNDSAMR INYYPLCQKP
PoGA20ox_4      YCDAMNSLSL GIMELLGLSL GVGQ-EYLRD FFEGNDSSMR INYYPPCQKP
PoGA20ox_5      YSEAMKKLSL VIFELLAISL GVDR-LHYRK FFEDGTSIMR QNYYPPCNNC
AtGA20ox_1      YCEAMSSLSL KIMELLGLSL GVKR-DYFRE FFEENDSIMR INYYPPCIKP
AtGA20ox_2      YCEAMSSLSL KIMELLGLSL GVNR-DYFRG FFEENDSIMR INHYPPCQTP
AtGA20ox_3      YAEAMNTLSL KIMELLGMSL GVER-RYFKE FFEDSDSIFR INYYPQCKQP
AtGA20ox_4      YAETMSNLSL KIMELLGMSL GIKR-EHFRE FFEDNESIFR INYYPKCKQP
AtGA20ox_5      FCDAMNGLVM DLMELLGISM GLKDRTYYRR FFEDGSGIFR QNYYPPCKQP
VvGA20ox_1      YCEAMSTLSL VIMELLGMSL GIGG-AHFRE FFEENDSIMR INYYPPCLKP
VvGA20ox_2      YCEAMSRLSL GIMELLGMSL GVGR-EYFRE FFEGNDSIMR INYYPPCQKP
VvGA20ox_3      YCDALKELSL GIMQLLAISL DVDS-SYYRK LFEDGYSIMR QNSYPPCKEA
VvGA20ox_4      YCQAMKDLSL VLMELLAISL GVDR-LHYRK FFEDGSSIMR QNYYPPCQEP
VvGA20ox_5      FCEAMKDLSL KIFKLLAISL NLEDTSYCEK FFEDGFAVLR QNYYPVCPES
Clustal Co      :.:::. * :  :::**.:*: .:    : .  ::: . . :*  * ** *
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Figura 17. Alinhamento de regiões das sequências proteicas de ortólogos de GA20ox, sendo PoGA20ox, de *Passiflora organensis*, AtGA20ox, de *Arabidopsis thaliana* e VvGA20ox, de *Vitis vinifera*. A linha Clustal Co mostra o grau de conservação entre as sequências, sendo representados por [*] os aminoácidos totalmente conservados, [:] altamente conservados e a ausência de símbolos indica que não há conservação entre os resíduos.

Os genes codificadores de GA2ox foram divididos em dois grupos, sendo um formado por *PoGA2ox7* e *PoGA2ox8* e seus ortólogos de *A. thaliana* e *V. vinífera*. Em

V. vinifera e *A. thaliana*, e outro por *PoGA2ox2, 3, 4a, 4b, 6a* e *6b*. Resultados similares foram observados por Jung et al. (2014).

Família gênica *GIBBERELLIN-INSENSITIVE DWARF1* (*GID1*)

A família gênica *GID1*, codificadora de receptores de giberelina, em outras espécies como *A. thaliana* (Nakajima et al. 2006) e *V. vinifera* (Acheampong et al. 2015), apresenta três genes, sendo *GID1a*, *GID1b* e *GID1c*. Geralmente, os ortólogos de GID1a e c estão agrupados enquanto os de GID1b encontram-se em um outro grupo. No entanto, em *P. organensis*, há um ortólogo de *GID1a* (ou *c*) e dois de *GID1b*, tendo ocorrido um evento de duplicação (Figura 18) após a divergência entre *Vitis*, *Arabidopsis* e *Passiflora* neste último caso.

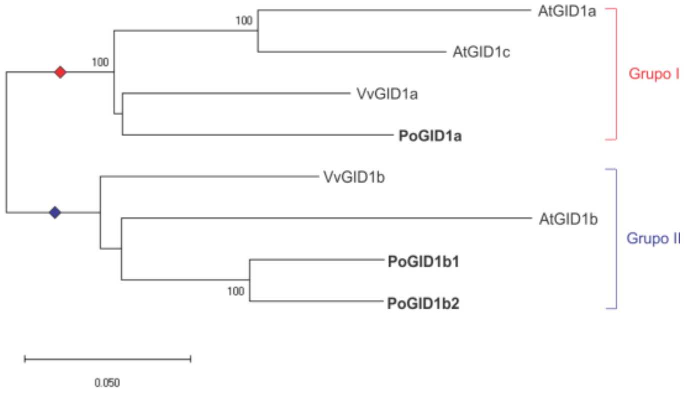


Figura 18. Árvore filogenética da família *GID1*, contendo sequencias de *Passiflora organensis* (Po) e os ortólogos de *Arabidopsis thaliana* (At) e *Vitis vinifera* (Vv).

A estrutura de todos os ortólogos de *P. organensis* foi semelhante à de *A. thaliana*, em torno de 1400 a 1800pb, com dois exons e um intron, tendo o primeiro em torno de 40pb, e o segundo em torno de 1200pb (Figura 19).

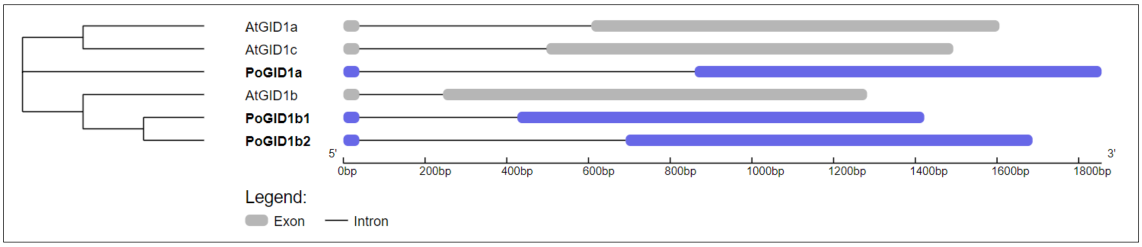
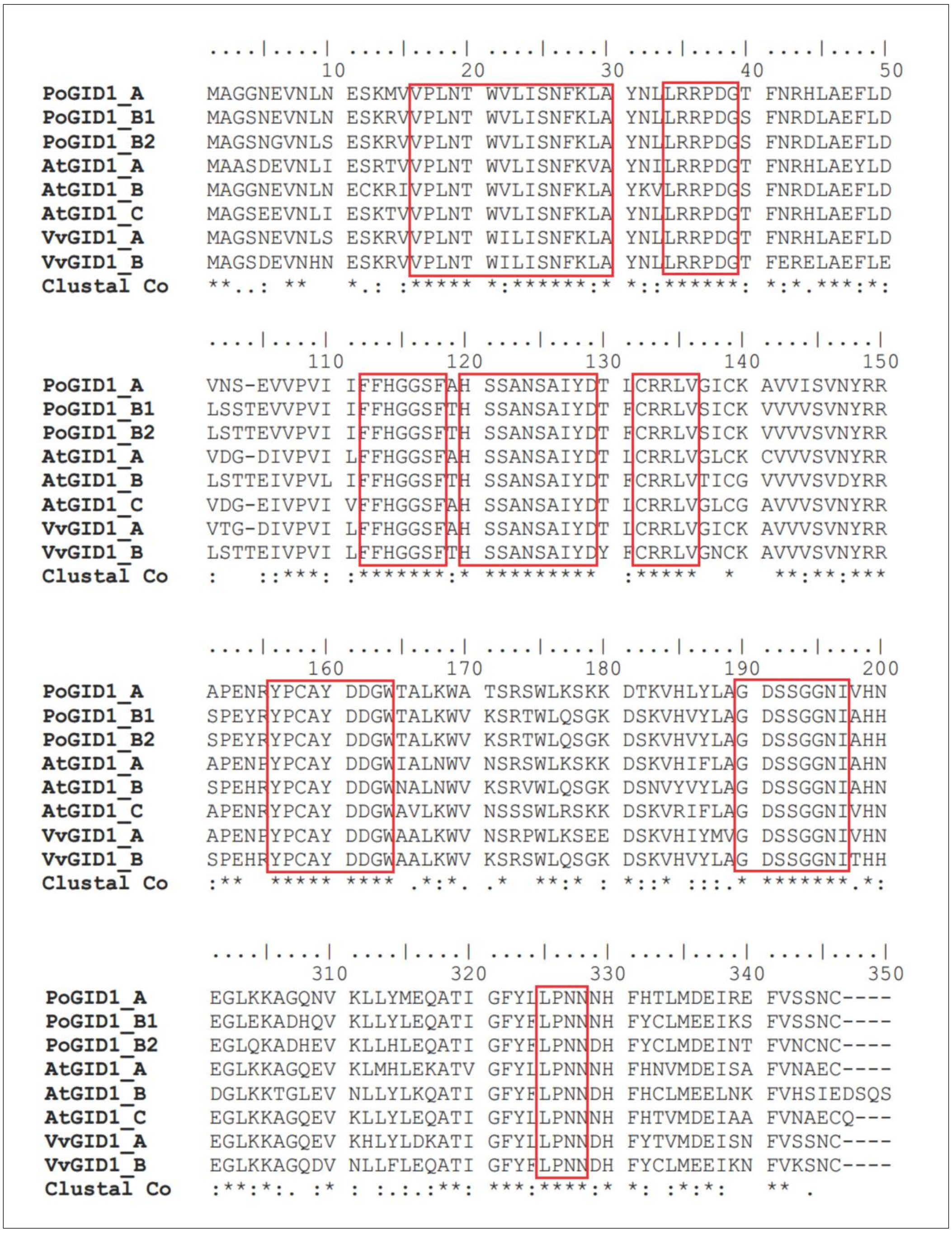


Figura 19. Estrutura dos genes da família *GID1* Genes em azul são de *Passiflora organensis* (Po) e em cinza de *Arabidopsis thaliana* (At).

Nos ortólogos putativos de GID1 foram observadas várias sequências 100% conservadas: VPLNTWVLISNFKLA, entre os resíduos 15 e 30; LRRPDG, entre os aminoácidos 34 e 39; FFHGGSF, entre 110 e 120; HSSANSAIYD, entre 120 e 130; CRRLV, entre 130 e 140; YPCAY, entre 155 e 165; GDSSGGNI, entre 190 e 200; e finalmente LPNN, entre os resíduos 325 e 330 (Figura 20).



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              ....|....| ....|....| ....|....| ....|....| ....|....|
                      10         20         30         40         50
PoGID1_A      MAGGNEVNLN ESKMVVPLNT WVLISNFKLA YNLLRRPDGT FNRHLAEFLD
PoGID1_B1     MAGSNEVNLN ESKRVVPLNT WVLISNFKLA YNLLRRPDGS FNRDLAEFLD
PoGID1_B2     MAGSNGVNLS ESKRVVPLNT WVLISNFKLA YNLLRRPDGS FNRDLAEFLD
AtGID1_A      MAASDEVNLI ESRTVVPLNT WVLISNFKVA YNILRRPDGT FNRHLAEYLD
AtGID1_B      MAGGNEVNLN ECKRIVPLNT WVLISNFKLA YKVLRRPDGS FNRDLAEFLD
AtGID1_C      MAGSEEVNLI ESKTVVPLNT WVLISNFKLA YNLLRRPDGT FNRHLAEFLD
VvGID1_A      MAGSNEVNLS ESKRVVPLNT WILISNFKLA YNLLRRPDGT FNRHLAEFLD
VvGID1_B      MAGSDEVNHN ESKRVVPLNT WILISNFKLA YNLLRRPDGT FERELAEFLE
Clustal Co    **..: **   *.: :***** *:******:* *::******: *:*.***:*:

              ....|....| ....|....| ....|....| ....|....| ....|....|
                     110        120        130        140        150
PoGID1_A      VNS-EVVPVI IFFHGGSFAH SSANSAIYDT ICRRLVGICK AVVISVNYRR
PoGID1_B1     LSSTEVVPVI IFFHGGSFTH SSANSAIYDT FCRRLVSICK VVVVSVNYRR
PoGID1_B2     LSTTEVVPVI IFFHGGSFTH SSANSAIYDT FCRRLVSICK VVVVSVNYRR
AtGID1_A      VDG-DIVPVI LFFHGGSFAH SSANSAIYDT ICRRLVGLCK CVVVSVNYRR
AtGID1_B      LSTTEIVPVL IFFHGGSFTH SSANSAIYDT FCRRLVTICG VVVVSVDYRR
AtGID1_C      VDG-EIVPVI VFFHGGSFAH SSANSAIYDT ICRRLVGLCG AVVVSVNYRR
VvGID1_A      VTG-DIVPVI LFFHGGSFAH SSANSAIYDT ICRRLVGICK AVVVSVNYRR
VvGID1_B      LSTTEIVPVI LFFHGGSFTH SSANSAIYDY FCRRLVGNCK AVVVSVNYRR
Clustal Co    :   ::***: :*******:* *********  :*****  *   **:**:***

              ....|....| ....|....| ....|....| ....|....| ....|....|
                     160        170        180        190        200
PoGID1_A      APENRYPCAY DDGWTALKWA TSRSWLKSKK DTKVHLYLAG DSSGGNIVHN
PoGID1_B1     SPEYRYPCAY DDGWTALKWV KSRTWLQSGK DSKVHVYLAG DSSGGNIAHH
PoGID1_B2     SPEYRYPCAY DDGWTALKWV KSRTWLQSGK DSKVHVYLAG DSSGGNIAHH
AtGID1_A      APENPYPCAY DDGWIALNWV NSRSWLKSKK DSKVHIFLAG DSSGGNIAHN
AtGID1_B      SPEHRYPCAY DDGWNALNWV KSRVWLQSGK DSNVYVYLAG DSSGGNIAHN
AtGID1_C      APENRYPCAY DDGWAVLKWV NSSSWLRSKK DSKVRIFLAG DSSGGNIVHN
VvGID1_A      APENPYPCAY DDGWAALKWV NSRPWLKSEE DSKVHIYMVG DSSGGNIVHN
VvGID1_B      SPEHRYPCAY DDGWAALKWV KSRSWLQSGK DSKVHVYLAG DSSGGNITHH
Clustal Co    :**  ***** **** .*:*. .*  **:* : *::* :::.* *******.*:

              ....|....| ....|....| ....|....| ....|....| ....|....|
                     310        320        330        340        350
PoGID1_A      EGLKKAGQNV KLLYMEQATI GFYLLPNNNH FHTLMDEIRE FVSSNC----
PoGID1_B1     EGLEKADHQV KLLYLEQATI GFYFLPNNNH FYCLMEEIKS FVSSNC----
PoGID1_B2     EGLQKADHEV KLLHLEQATI GFYFLPNNDH FYCLMDEINT FVNCNC----
AtGID1_A      EGLKKAGQEV KLMHLEKATV GFYLLPNNNH FHNVMDEISA FVNAEC----
AtGID1_B      DGLKKTGLEV NLLYLKQATI GFYFLPNNDH FHCLMEELNK FVHSIEDSQS
AtGID1_C      EGLKKAGQEV KLLYLEQATI GFYLLPNNNH FHTVMDEIAA FVNAECQ---
VvGID1_A      EGLKKAGQEV KHLYLDKATI GFYLLPNNDH FYTVMDEISN FVSSNC----
VvGID1_B      EGLKKAGQDV NLLFLEQATI GFYFLPNNDH FYCLMEEIKN FVKSNC----
Clustal Co    :**:*:. :* : :.:.:**: ***:****:* *: :*:*:   ** .
```

Figura 20. Alinhamento de regiões das sequências proteicas de ortólogos de GID1, sendo PoGID1, de *Passiflora organensis*, AtGID1, de *Arabidopsis thaliana* e VvGID1, de *Vitis vinifera.* A linha Clustal Co mostra o grau de conservação entre as sequências, sendo representados por [*] os aminoácidos totalmente conservados, [:] altamente conservados e a ausência de símbolos indica que não há conservação entre os resíduos.

Genes *DELLA*

As proteínas DELLA são repressores transcricionais reguladas por giberelina (Briones-Moreno et al. 2017) PoDELLA1 e PoDELLA3 ficaram agrupados enquanto PoDELLA2a e PoDELLA2b estavam em um outro grupo (Figura 21). Em comparação com *A. thaliana*, houve uma redução do número de genes, que apresentava cinco (*AtDELLA1, 2, 3, 4* e *5*), contudo houve uma duplicação do ortólogo correspondente ao *AtDELLA2* (Figura 21). As duplicações de genes são consideradas uma das principais forças motrizes na evolução dos genomas (Xu et al. 2020). Os genes DELLA apresentam variações quanto ao número nas difetentes espécies. Enquanto no tomateiro (*Solanum lycopersicum*) há apenas um gene *DELLA* (Bassel et al. 2004), em *P. organensis*, no presente trabalho, foram identificados quatro DELLA e em *Arabidopsis* há cinco DELLA com funções bem estabelecidas e nomenclaturas distintas. Contudo, utilizamos a nomenclatura DELLA para todos os genes de *P. organensis* identificados porque precisaríamos de análises adicionais para identificar os possíveis papeis fisiológicos de cada um dos ortólogos.

Em *Arabidopsis*, o AtDELLA1 é denominado GA INSENSITIVE (GAI) (Peng et al. 1997) e AtDELLA3 é o REPRESSOR OF GA1–3 (RGA) (Silverstone et al. 1998). RGA e GAI possuem funções similares, reprimindo o crescimento do caule (Dill et al. 2001). Os ortólogos PoDELLA1 e PoDELLA3 que identificamos, por similaridade das sequências, foram agrupados com os de *Arabidopsis* e *V. vinifera*. Então estes podem ser os GAI e RGA de P. organensis, embora sejam necessárias análises posteriores para diferenciar os dois genes, visto que há diferenciação funcional. Os outros três genes DELLA de Arabidopsis são denominados RGA-LIKE: o AtDELLA2 no presente trabalho é o RGL1, AtDELLA4 é o RGL2 e o AtDELLA5 é o RGL3 (Lee et al. 2002). Estudos anteriores identificaram que o RGL1 e RGL2 estariam relacionados ao desenvolvimento floral (Wen e Chang 2002; Cheng et al. 2004). Enquanto RGL2 e RGL3 atuariam no controle da germinação das sementes (Lee et al. 2002; Piskurewicz e Lopez-Molina 2009). Identificamos, por similaridade das sequências, um PoDELLA2 e um PoDELLA5, que poderiam corresponder ao RGL1 e RGL3 de Arabidopsis. Contudo, como as funções destes genes já estão bem estabelecidas, seriam necessárias análises específicas para identificar com precisão quais seriam esses genes em P. organensis.

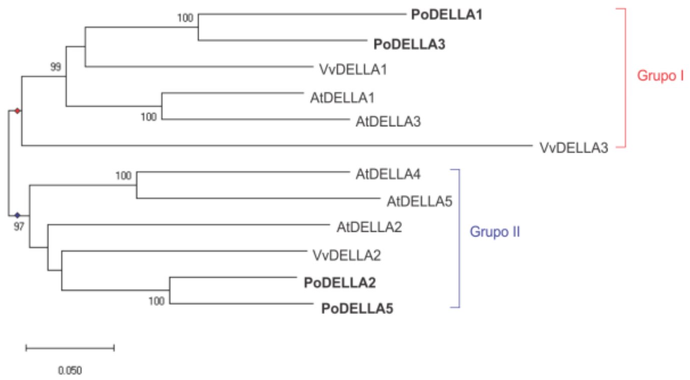


Figura 21. Árvore filogenética da família DELLA, contendo genes de *Passiflora organensis* (Po) e os ortólogos de *Arabidopsis thaliana* (At) e *Vitis vinifera* (Vv).

Os genes *DELLA* em *P. organensis* não apresentavam íntrons (Figura 22), assim como em *A. thaliana* e *V. vinifera* (Acheampong et al. 2015).

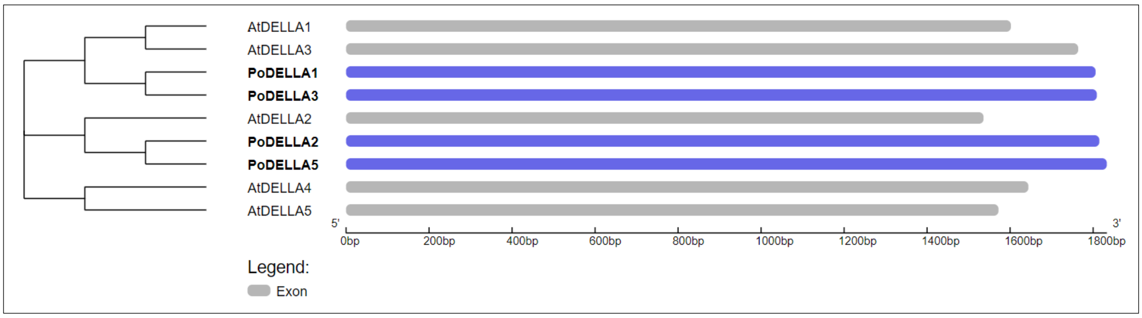
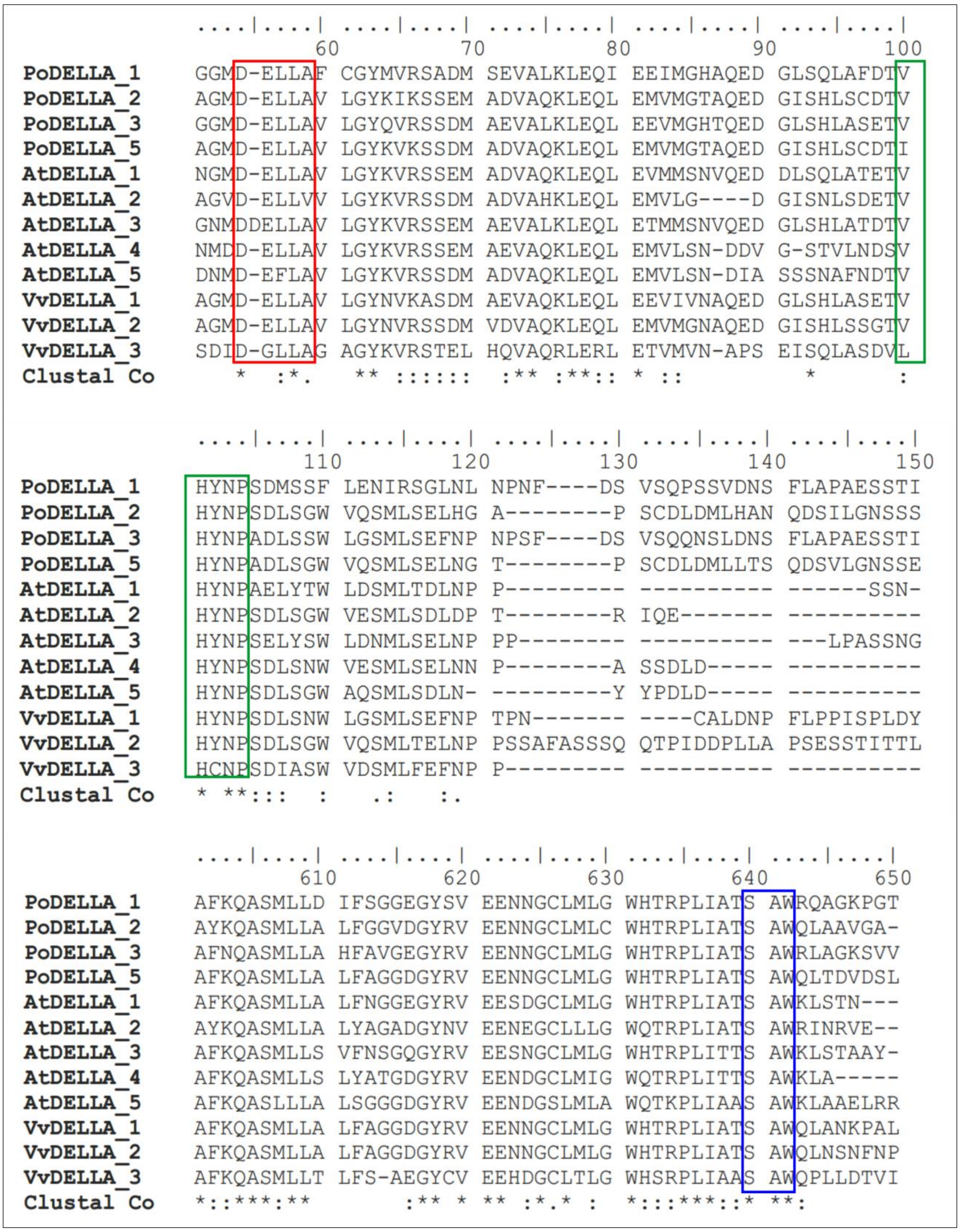


Figura 22. Estrutura dos genes da família *DELLA*. Genes em azul são de *Passiflora organensis* (Po) e em cinza de *Arabidopsis thaliana* (At).

Os ortólogos putativos de *P. organensis* da família proteica DELLA apresentaram três regiões altamente conservadas: DELLA, entre os aminoácidos 54 e 60; VHYNP, entre os resíduos 100 e 105; e SAW, entre os resíduos 640 e 645 (Figura 23). A região DELLA, que dá nome à família, fica localizada na região N-terminal, que é fortemente conservado entre todas as espécies de plantas superiores (Dill et al. 2001). Contudo, as outras espécies que comparamos nesste estudo apresentaram poucas variações, AtDELLA2, AtDELLA5 e VvDELLA3, e isso já foi relatado em outras espécies (Wang et al. 2020).

Os motivos DELLA, VHYNP (Cassani et al. 2009) e SAW estão possivelmente envolvidos na ligação com GID1 (Vera-Sirera et al. 2016).



```
               ....|....| ....|....| ....|....| ....|....| ....|....|
                        60         70         80         90        100
PoDELLA_1      GGMD-ELLAF CGYMVRSADM SEVALKLEQI EEIMGHAQED GLSQLAFDTV
PoDELLA_2      AGMD-ELLAV LGYKIKSSEM ADVAQKLEQL EMVMGTAQED GISHLSCDTV
PoDELLA_3      GGMD-ELLAV LGYQVRSSDM AEVALKLEQL EEVMGHTQED GLSHLASETV
PoDELLA_5      AGMD-ELLAV LGYKVKSSDM ADVAQKLEQL EMVMGTAQED GISHLSCDTI
AtDELLA_1      NGMD-ELLAV LGYKVRSSEM ADVAQKLEQL EVMMSNVQED DLSQLATETV
AtDELLA_2      AGVD-ELLVV LGYKVRSSDM ADVAHKLEQL EMVLG----D GISNLSDETV
AtDELLA_3      GNMDDELLAV LGYKVRSSEM AEVALKLEQL ETMMSNVQED GLSHLATDTV
AtDELLA_4      NMDD-ELLAV LGYKVRSSEM AEVAQKLEQL EMVLSN-DDV G-STVLNDSV
AtDELLA_5      DNMD-EFLAV LGYKVRSSDM ADVAQKLEQL EMVLSN-DIA SSSNAFNDTV
VvDELLA_1      AGMD-ELLAV LGYNVKASDM AEVAQKLEQL EEVIVNAQED GLSHLASETV
VvDELLA_2      AGMD-ELLAV LGYNVRSSDM VDVAQKLEQL EMVMGNAQED GISHLSSGTV
VvDELLA_3      SDID-GLLAG AGYKVRSTEL HQVAQRLERL ETVMVN-APS EISQLASDVL
Clustal Co        *  :*.   ** ::::::  :** :**:: * ::         *      :

               ....|....| ....|....| ....|....| ....|....| ....|....|
                       110        120        130        140        150
PoDELLA_1      HYNPSDMSSF LENIRSGLNL NPNF----DS VSQPSSVDNS FLAPAESSTI
PoDELLA_2      HYNPSDLSGW VQSMLSELHG A--------P SCDLDMLHAN QDSILGNSSS
PoDELLA_3      HYNPADLSSW LGSMLSEFNP NPSF----DS VSQQNSLDNS FLAPAESSTI
PoDELLA_5      HYNPADLSGW VQSMLSELNG T--------P SCDLDMLLTS QDSVLGNSSE
AtDELLA_1      HYNPAELYTW LDSMLTDLNP P--------- ---------- ------SSN-
AtDELLA_2      HYNPSDLSGW VESMLSDLDP T--------R IQE------- ----------
AtDELLA_3      HYNPSELYSW LDNMLSELNP PP-------- ---------- ---LPASSNG
AtDELLA_4      HYNPSDLSNW VESMLSELNN P--------A SSDLD----- ----------
AtDELLA_5      HYNPSDLSGW AQSMLSDLN- ---------Y YPDLD----- ----------
VvDELLA_1      HYNPSDLSNW LGSMLSEFNP TPN------- ----CALDNP FLPPISPLDY
VvDELLA_2      HYNPSDLSGW VQSMLTELNP PSSAFASSSQ QTPIDDPLLA PSESSTITTL
VvDELLA_3      HCNPSDIASW VDSMLFEFNP P--------- ---------- ----------
Clustal Co     * **:::  :   .:   :.

               ....|....| ....|....| ....|....| ....|....| ....|....|
                       610        620        630        640        650
PoDELLA_1      AFKQASMLLD IFSGGEGYSV EENNGCLMLG WHTRPLIATS AWRQAGKPGT
PoDELLA_2      AYKQASMLLA LFGGVDGYRV EENNGCLMLC WHTRPLIATS AWQLAAVGA-
PoDELLA_3      AFNQASMLLA HFAVGEGYRV EENNGCLMLG WHTRPLIATS AWRLAGKSVV
PoDELLA_5      AFKQASMLLA LFAGGDGYRV EENNGCLMLG WHTRPLIATS AWQLTDVDSL
AtDELLA_1      AFKQASMLLA LFNGGEGYRV EESDGCLMLG WHTRPLIATS AWKLSTN---
AtDELLA_2      AYKQASMLLA LYAGADGYNV EENEGCLLLG WQTRPLIATS AWRINRVE--
AtDELLA_3      AFKQASMLLS VFNSGQGYRV EESNGCLMLG WHTRPLITTS AWKLSTAAY-
AtDELLA_4      AFKQASMLLS LYATGDGYRV EENDGCLMIG WQTRPLITTS AWKLA-----
AtDELLA_5      AFKQASLLLA LSGGGDGYRV EENDGSLMLA WQTKPLIAAS AWKLAAELRR
VvDELLA_1      AFKQASMLLA LFAGGDGYRV EENNGCLMLG WHTRPLIATS AWQLANKPAL
VvDELLA_2      AFKQASMLLA LFAGGDGYRV EENNGCLMLG WHTRPLIATS AWQLNSNFNP
VvDELLA_3      AFKQASMLLT LFS-AEGYCV EEHDGCLTLG WHSRPLIAAS AWQPLLDTVI
Clustal Co     *::***:**       :** * ** :*.* :  *:::***::* **:
```

Figura 23. Alinhamentos de regiões das sequências proteicas de ortólogos de DELLA, sendo PoDELLA, de *Passiflora organensis*, AtDELLA de *Arabidopsis thaliana* e VvDELLA, de *Vitis vinifera*. A linha Clustal Co mostra o grau de conservação entre as sequências, sendo representados por [*] os aminoácidos totalmente conservados, [:] altamente conservados e a ausência de símbolos indica que não há conservação entre os resíduos.

Conclusões

Identificamos os genes relacionados a metabolismo e resposta a citocininas e giberelinas, que incluíram oito genes PoIPT, dez PoLOG, nove PoCKX, dez PoRRs do tipo A, 11 Po RRs do tipo B, quatro GA3oxs, cinco GA20oxs, oito GA2oxs, três

PoGID1 e quatro PoDELLA. As análises filogenéticas, de estrutura gênica e de alinhamento das sequências proteicas, revelaram que estas famílias gênicas em *P. organensis* são conservadas e similares em número e estrutura às de *Arabidopsis*. Para a maioria das famílias gênicas analisadas, as funções de cada parálogo não são bem conhecidas, com exceção dos genes DELLA. Nossos achados serão úteis para estudos futuros para inferir as funções destes genes e compreender seus papéis no desenvolvimento de espécies de *Passiflora* bem como de outras espécies vegetais.

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CAPÍTULO IV - Análise do padrão de expressão gênica dos genes de metabolismo e resposta a giberelinas em *Passiflora edulis*

Resumo

As giberelinas (GAs) controlam o crescimento e diversos aspectos do desenvolvimento de vegetais, inclusive a transição da fase juvenil para a adulta vegetativa. Analisamos por meio de RT-qPCR (Reverse Transcription quantitative PCR) a expressão relativa de genes relacionados ao metabolismo e à resposta a GAs em plantas de *P. edulis*. Comparamos plantas submetidas a pulverizações de GA_3 em diferentes concentrações e também plantas tratadas com paclobutrazol. O gene de biossíntese de GA analisado, o *PoGA3ox3*, teve uma diminuição gradual em sua expressão quanto maior foi a dose de GA_3 aplicada, enquanto o gene *PoGA2ox8*, envolvido no catabolismo de GA, e os *PoDELLA2*, *PoDELLA3* e *PoDELLA5*, de resposta às vias de sinalização de GA, tiveram aumento em sua expressão. A aplicação de paclobutrazol causou efeito oposto ao da aplicação exógena de GA_3 sem efeito de dose. Os resultados obtidos contribuem para a compreensão de como as GAs atuam durante o desenvolvimento de *Passiflora* e podem servir como base para estudos de modulação dos níveis destes genes para controlar a transição da fase juvenil para a adulta vegetativa.

Abstract

Gibberellins (GAs) control the growth and several aspects of plant development, including the transition from juvenile to adult vegetative phase. We analyzed by RT-qPCR (Reverse Transcription quantitative PCR) the relative expression of genes related to the metabolism and response to GAs in *P. edulis* plants. We compared plants subjected to spraying of GA_3 at different concentrations and also plants treated with paclobutrazol. The GA biosynthesis gene analyzed, *PoGA3ox3*, had a gradual decrease in its expression followin the increase in the dose of GA3 applied, while *PoGA2ox8*, a GA catabolism gene, and the *PoDELLA2*, *PoDELLA3* and *PoDELLA5*, considered GA signalling pathway response genes, had an increase in their expression. Paclobutrazol had the opposite effect to that of GA_3 although no dose effect was observed. These results contribute to the understanding of how GAs act during *Passiflora* development

and can serve as a basis for studies aiming to control the transition from the juvenile to the vegetative adult phase in passion fruit.

Introdução

As giberelinas (GAs) são uma importante classe de fitormônios que controlam vários aspectos do desenvolvimento vegetal, como germinação das sementes, crescimento do caule e das raízes, expansão das folhas e florescimento (Yamaguchi 2008; Ramon 2021). Quimicamente, as GAs são ácidos carboxílicos tetracíclicos produzidos a partir da via dos terpenoides (Hedden e Thomas 2012) a partir de um esqueleto de cinco carbonos e dois grupos fosfato, o isopentenil pirofosfato (IPP) (Lange 1998). Sua atividade biológica mais conhecida é o crescimento do caule, sendo que sua descoberta ocorreu por conta de uma doença em arroz, na qual as plantas apresentavam um crescimento excessivo provocado pelas GAs produzidas pelo fungo *Giberella fujikuroi*. Além de seus efeitos bem conhecidos no crescimento de órgãos vegetais, através da expansão celular (Hedden e Thomas 2012), germinação das sementes (Ogawa et al. 2003) e desenvolvimento dos frutos (Serrani et al. 2007; Csukasi et al. 2011), as GAs possuem grande importância no ciclo de vida das plantas podendo estimular (Blázquez et al. 1998; Mutasa-Göttgens e Hedden 2009; Liu et al. 2020) ou inibir (An et al. 2008; Sobol et al. 2014; Li et al. 2018) o desenvolvimento floral além de controlarem o padrão de ramificação de diferentes espécies de vegetais durante a fase juvenil (Du et al. 2017; Cheng et al. 2021).

Existem cerca de 136 GAs identificadas em diferentes espécies de plantas, fungos e bactérias (MacMillan 2001; Gao 2017). No entanto, apenas quatro são bioativas: GA_1, GA_3, GA_4 e GA_7 (Hedden e Sponsel 2015). A biossíntese de GAs ocorre em várias etapas, compartimentalizadas em três locais nas células: nos cloroplastos ocorre a formação do ent-caureno a partir de geranilgeranil difosfato (GGDP) (Aach et al. 1997); posteriormente, no retículo endoplasmático, há formação do GA12 a partir do ent-caureno (Hedden 1997; Lange 1998); e por fim, a formação de GAs bioativas no citoplasma (Hedden 1997; Suzuki et al. 1992).

As enzimas que catalisam diretamente os processos de ativação e inativação das GAs são GA oxidases que pertencem às famílias das dioxigenases dependentes de 2-oxoglutarato (2-ODDs) (Lange e Lange 2020). As GA20OXIDASES (GA20ox) e GA3OXIDASES (GA3ox) catalisam as etapas finais na formação de GAs bioativas, principalmente GA1 e GA4 (Hedden e Phillips 2000). Portanto são enzimas anabólicas no metabolismo de GA. Há ainda outras classes de GA OXIDASES anabólicas: as GA7OXIDASES, identificadas em abóbora, *Cucurbita maxima* (Lange 1997), e pepino, *Cucumis sativus* (Lange et al. 2013) e as GAS2, descobertas recentemente, que também utilizam GA12 como substrato para gerar GAs bioativas (Liu et al. 2019; Lange e Lange 2020). Dentre as enzimas que agem no catabolismo de GAs, as principais são as GA2OXIDASES (GA2ox), que são também 2-ODDs (Hedden e Thomas 2012; Lange e Lange 2020). As GA2ox inativam as GAs bioativas convertendo-as em formas inativas por β-hidroxilação (Thomas et al. 1999; Hedden e Phillips 2000). Elas são geralmente classificadas como C19-GA2oxs ou C20-GA2oxs, dependendo do número de átomos de carbono dos substratos sobre os quais agem (Hedden e Thomas 2012; Lange e Lange 2020).

Vários estudos de identificação e expressão gênica têm sido realizados buscando identificar as famílias *GA20ox*, *GA3ox* e *GA2ox*, em *Arabidopsis* (Rieu et al. 2008; Li et al. 2019), e sobretudo em espécies vegetais de interesse agronômico e comercial, como videira (*Vitis vinifera)* (Giacomelli et al. 2013; Jung et al. 2014; He et al. 2019), morango (*Fragaria vesca)* (Tenreira et al. 2017), ervilha (*Pisum sativum)* (Reinecke et al. 2013), arroz (*Oryza sativa)* (Sakamoto et al. 2004), juta (*Corchorus* sp.) (Honi et al. 2020), milho (*Zea mays)* (Song et al. 2011) e melancia (*Citrullus lanatus) (*Sun et al. 2020). Há evidências de que os parálogos dentro destas famílias gênicas possuem redundância funcional (Sakamoto et al. 2004; He et al. 2019).

Análises de expressão dos genes relacionados ao metabolismo de GAs durante as transições de fases possibilitam a compreensão de como essa classe de fitormônios atua na regulação destes processos. Em *Vitis vinifera*, houve diminuição da expressão dos genes anabólicos e aumento da expressão dos genes catabólicos das vias de GAs quando as plantas foram submetidas a aplicações de GAs exógenas antes do florescimento (Jung et al. 2014). Por outro lado, *VvGA3ox* e *VvGA20ox*, de biossíntese de GAs foram regulados positivamente sob tratamento com uniconazol, um inibidor da biossíntese de GA (He et al. 2019). Estes resultados sugerem que a aplicação de GAs exógenas interferem no metabolismo das GAs alterando o nível de transcrição e consequentemente o momento do desenvolvimento da inflorescência em videiras.

No desempenho de suas funções, as GAs agem em resposta aos sinais ambientais e endógenos, que podem regular a biossíntese, desativação, percepção e resposta, sendo que estes sinais podem agir em vários pontos das vias (Hedden e

Thomas 2012). Os mecanismos moleculares pelos quais esses hormônios são percebidos e como essa informação é traduzida em alterações transcricionais foi elucidado há muitos anos em plantas: as giberelinas são percebidas pelo receptor nuclear GIBBERELLIN INSENSITIVE DWARF1 (GID1), descoberto em arroz (Ueguchi-Tanaka et al. 2005). Com o aumento da concentração de GA e sua ligação ao GID1, este complexo interage com o complexo de poliubiquitinação SCF-GID2, que provoca a degradação das proteínas DELLA da família GRAS de fatores de transcrição (Itoh et al. 2003; Sasaki et al. 2003). Como as proteínas DELLA reprimem o mecanismo molecular de ação das GAs, não havendo mais repressão da transcrição, os genes regulados pelas GAs podem agir (Harberd et al. 2009). Os GAs bioativos são justamente caracterizados pela capacidade de interagir com o GID1 para iniciar a degradação de proteínas DELLA que reprimem o mecanimo de ação das GAs (Ueguchi-Tanaka et al. 2007).

Em *Arabidopsis* foram identificados três *GID1* que possivelmente possuem funções redundantes, pois os mutantes únicos se desenvolveram normalmente enquanto os mutantes triplos tiveram fenótipo anão (Griffiths et al. 2006). Além disso, esses mutantes triplos tiveram acúmulo da proteína DELLA do tipo REPRESSOR DE GA1-3 (RGA). As proteínas DELLA de *Arabidopsis* são cinco e possuem papéis geneticamente separáveis no controle do crescimento do caule e do tamanho do meristema da inflorescência (Serrano-Mislata et al. 2017). As proteínas DELLA influenciam na atividade dos meristemas axilares e, portanto podem interferir nas transições de fases. Sua participação na regulação dos meristemas axilares ocorre pela interação com a SQUAMOSA-PROMOTER BINDING PROTEIN LIKE 9 (SPL9) que reprime a expressão do gene *LATERAL SUPPRESSOR* (*LAS*), inibidor da ativação destes meristemas (Zhang et al. 2020).

Alguns estudos têm sido realizados analisando a expressão de genes relacionados a metabolismo e resposta a GAs para compreender como as GAs influenciam no florescimento e no crescimento vegetativo em diferentes espécies. No pinhão manso, *Jatropha curcas* L., durante a transição da fase adulta vegetativa para a reprodutiva, Os níveis de expressão dos genes, *JcGA3ox3* e *JcGID1C*, respectivamente, foram reduzidos, enquanto o de *JcGA2ox8*, foi elevado durante a transição floral (Li et al. 2018). Estes resultados evidenciaram que as GAs inibem o florescimento em *J. curcas*. Em pêssego, *Prunus persica*, foram identificados sete genes da família *GA2ox*, e superexpressos em plantas de tabaco, que apresentaram fenótipo anão (Cheng et al. 2021). O tratamento com GA_3 exógeno ativou a expressão de todos os sete genes

PpGA2ox. Estes resultados permitem manipular os níveis endógenos de GAs no pêssego, e assim controlar o crescimento dos ramos, reduzindo a necessidade de poda na espécie.

No gênero *Passiflora*, são conhecidos os efeitos morfológicos das GAs na transição para a fase reprodutiva em *P. edulis* (Sobol et al. 2014) e da fase juvenil para a adulta vegetativa em *P. organensis* (ver Capítulo II). Também já foram identificados os genes envolvidos na biossíntese, catabolismo, sinalização e resposta a GAs em *P. organensis* (ver Capítulo III). Neste capítulo, temos como objetivo analisar a expressão dos genes de metabolismo e resposta as GAs na transição da fase juvenil para a adulta vegetativa. Os resultados obtidos podem permitir a modulação dos níveis de GAs e assim regular a arquitetura das plantas, pela quantidade de ramos e inflorescências produzidas. Portanto, podem ser de grande utilidade para a produção vegetal do maracujazeiro, bem como de outras espécies de interesse agronômico.

Material e Métodos

Estabelecimento dos ensaios e aplicação dos fitormônios

Os ensaios foram conduzidos em casa de vegetação, do Instituto de Biologia da Unicamp, na cidade de Campinas-SP, entre os meses de setembro e novembro de 2019. As plantas de *P. edulis* utilizadas foram provenientes de sementes da variedade FB 300 (uma doação de Viveiros Flora Brasil) plantadas em vasos com composto orgânico Genesolo, Genefértil® (Composição: Bagaço de cana, palha de café, turfa, rocha calcárea, estercos e camas de aviário, cinzas, resíduo orgânico industrial papel/celulose e resíduo orgânico agroindústrial classe B) sendo transplantadas duas plantas para cada vaso.

Avaliamos sete tratamentos com diferentes doses de GA. Cada tratamento foi aplicado a dez plantas (repetições):

- três tratamentos consistiram em aplicações de ácido giberélico (GA_3) nas concentrações: 1,0; 10,0 ou 100,0 μM;
- três tratamentos consistiram em uma única aplicação de paclobutrazol (PAC), nas concentrações: 1,0; 10,0 ou 100,0 μM;
- e um grupo controle (que não recebeu aplicações de GA_3 nem de PAC).

O delineamento experimental foi inteiramente casualizado, com os vasos distribuídos nas mesas aleatoriamente. Após dois meses desde o plantio, as plantas dos tratamentos com giberelina receberam pulverizações diárias com as soluções de GA_3 e surfactante Tween-20 (duas gotas a cada 100ml de solução) durante três semanas. Durante a primeira semana, foram realizadas duas aplicações diárias do fitormônio, sendo uma pela manhã e outra no período da tarde. Na segunda e na terceira semanas, as plantas receberam uma única pulverização diária de GA_3. As plantas dos tratamentos com PAC tiveram as soluções de PAC aplicadas diretamente na terra, no dia em que o ensaio foi estabelecido. Três semanas (21 dias) após os tratamentos, foi coletada toda a parte aérea das plantas, congeladas em nitrogênio líquido e mantidas em biofreezer para as análises de expressão gênica com RT-qPCR. Quando coletadas, todas as plantas estavam em fase juvenil.

Extração de RNA e RT-qPCR

Cada planta de *P. edulis* correspondeu a uma amostra biológica. A extração foi realizada com o kit RNeasy Plant Mini Kit com RNase free DNase I (Qiagen). Posteriormente, os cDNAs foram sintetizados utilizando o kit SuperScript III RT (Invitrogen) de acordo com as instruções do fabricante. As concentrações dos RNAs e dos cDNAs foram medidas com o spectofotômetro Nanodrop 2000. Os valores ideais considerados de concentração de RNA e cDNA foram de aproximadamente 200ng/µL e a qualidade das amostras foi medida pelas razões A260/280 e A260/230 (Desjardins e Conklin 2010), considerando os valores ideais da razão A260/280 para cDNA como sendo ~1,8, e para RNA, ~2,0 e a razão A260/230 como sendo ideal entre 2,0 e 2,2 para ambos os ácidos nucleicos. As amostras não-conforme com estas caracterísitcas de qualidade foram descartadas.

Os primers para a RT-qPCR foram obtidos a partir das sequências genômicas dos genes descritos no Capítulo III, cujas sequências encontram-se no Apêndice C. Os primers foram desenhados manualmente e com o auxílio do software Primer3. Foram desenhados primers para 27 genes (Tabela 1 e Apêndice B). Contudo apenas cinco foram analisados (Tabela 1).

Tabela 1. Sequências dos primers dos genes de referência (PeCAC e PeSAND (Scorza, 2015)) e dos genes do metabolismo e resposta a giberelinas (obtidos a partir das sequências de *Passiflora organensis*) utilizados nas qRT-PCRs realizadas neste estudo.

Gene	**Tipo**	**Sequência do primer**	**Tamanho do transcrito (pb)**
PeCAC_F	Fw	TCAAGAGGGAGTGCGTTCAC	90
PeCAC_R	Rw	CAACCAACAGCGCCTGTAAC	
PeSAND_F	Fw	GGAGCTGCTTCTCCCCATTT	78
PeSAND_R	Rw	AGGGCCACCAATTCCAATGA	
PoDELLA2F2	Fw	GCCGCCGTGGGTGCATGATA	100
PoDELLA2R2	Rw	ATCCACTCGCCATCCAACTC	
PoDELLA3F1	Fw	AGGAGAACAACGGGTGTTTG	137
PoDELLA3R1	Rw	GACCTCGACTCGCACCTAGT	
PoDELLA5F2	Fw	ACCGACGTCGATTCATTGTA	100
PoDELLA5R2	Rw	ATACGCTCGCCGTTAACTCA	
PoGA2ox8F1	Fw	GCCTACTTCCTCTGCCCTTC	140
PoGA2ox8R1	Rw	GGAAGGCCTATTTTGTGACC	
PoGA3ox3F1	Fw	GTCCCGTGACATGGAAAGAT	124
PoGA3ox3R1	Rw	GCATCTTTGCTGACCAATGC	

As reações foram feitas no StepOnePlus Realtime PCR system (Applied Biosystems). Utilizamos dois genes de referência, segundo indicado na literatura (Scorza 2015). Foram eles: CLATHRIN ADAPTOR COMPLEX (CAC) e MONENSIN SENSIVITY 1/SAND family protein (SAND).

Para cada reação foi utilizada a seguinte fórmula, totalizando um volume de 10 µL:

- 1 µL de cDNA (100 ng/µL)
- 6 µL de SYBR Green (Applied Biosystems)
- 0,2 µL do primer *forward* (10 µM)
- 0,2 µL do primer *reverse* (10 µM)
- 2,6 µL de água DEPC

Para os controles negativos adicionou-se 1 µL de água DEPC em lugar do cDNA. As reações foram realizadas em três replicatas técnicas. O protocolo da amplificação consistiu em 40 ciclos de 95 °C por 10 min, 95 °C por 15 s, 60 °C por 1 min, 95 °C por 15 s, 60 °C por 1 min e 95 °C por 15 s.

Quando foi observado apenas um pico na curva de *melting*, o primer foi considerado específico (Figura 1). Dois ou mais picos indicavam que o primer não era específico. Nestes casos, foi necessário desenhar novos primers (Figura 2).

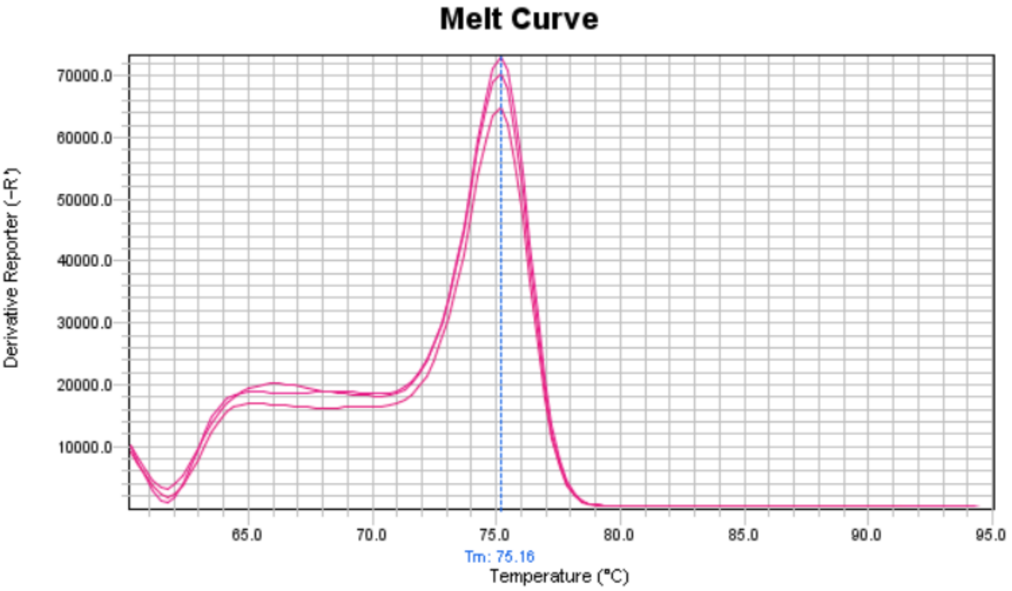

Figura 1. Exemplo de amplificação com primer específico, mostrando apenas um pico na curva de melting. As três linhas correspondem às três replicatas técnicas. Os primers utilizados foram os específicos para o gene PoDELLA5, com uma amostra de cDNA de *P. edulis.*

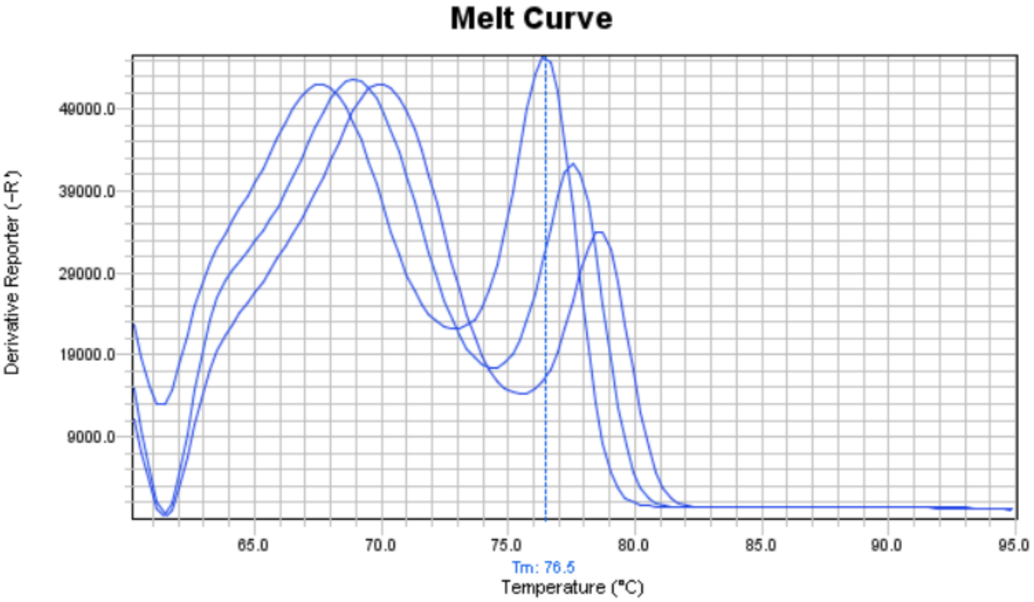

Figura 2. Exemplo de amplificação com primer inespecífico, mostrando dois picos na curva de melting. As três linhas correspondem às três replicatas técnicas Os primers utilizados foram os desenhados para o gene PoDELLA2, com uma amostra de cDNA de *P. edulis.* Estes primers não foram aprovados, tendo sido desenhado um novo par de primers para o mesmo gene.

As curvas de melting obtidas das replicatas de cada tratamento para cada gene estão no Apêndice E.

A partir dos valores de *Cycle Threshold* (CT) obtidos, foram calculados os níveis de expressão relativa dos genes, utilizando o método $2^{\Delta\Delta Ct}$, descrito por Livak e Schmittgen (2001). Com os valores de expressão relativa obtidas, foram feitas as análises estatísticas, utilizando o software R-4.0.5 (R Core Team). Os dados foram submetidos a uma análise de variância (ANOVA) e posteriormente ao teste de Tukey com nível de significância de 5%.

Resultados e Discussão

Com o aumento da concentração de GA_3 nos tratamentos, houve redução da expressão de *PoGA3ox3* (Figura 3A). Enquanto as plantas que receberam PAC em maior concentração, tiveram maior expressão deste gene. Contudo, os tratamentos pac10 e pac1 causaram uma menor expressão de *PoGA3ox3* do que o observado para as plantas controle, indicando que estas concentrações não foram suficientes para efetivar o efeito fisiológico observado na maior dose.

Por outro lado, o gene *PoGA2ox8* teve sua expressão aumentada, de acordo com o aumento na concentração de GA_3 nos tratamentos (Figura 3B). Os tratamentos ga10 e ga100 tiveram diferença estatisticamente significativa, demonstrando que quanto maior foi a concentração de giberelina aplicada, maior o efeito sobre o aumento da expressão gênica de *PoGA2ox8*. As plantas que receberam aplicações de PAC, tiveram menor expressão de *PoGA2ox8* que as plantas controle, embora este efeito não tenha sido estatisticamente significativo pelo teste de Tukey. Portanto, o paclobutrazol não apresentou efeito de dose sobre a expressão de *PoGA2ox8* neste estudo.

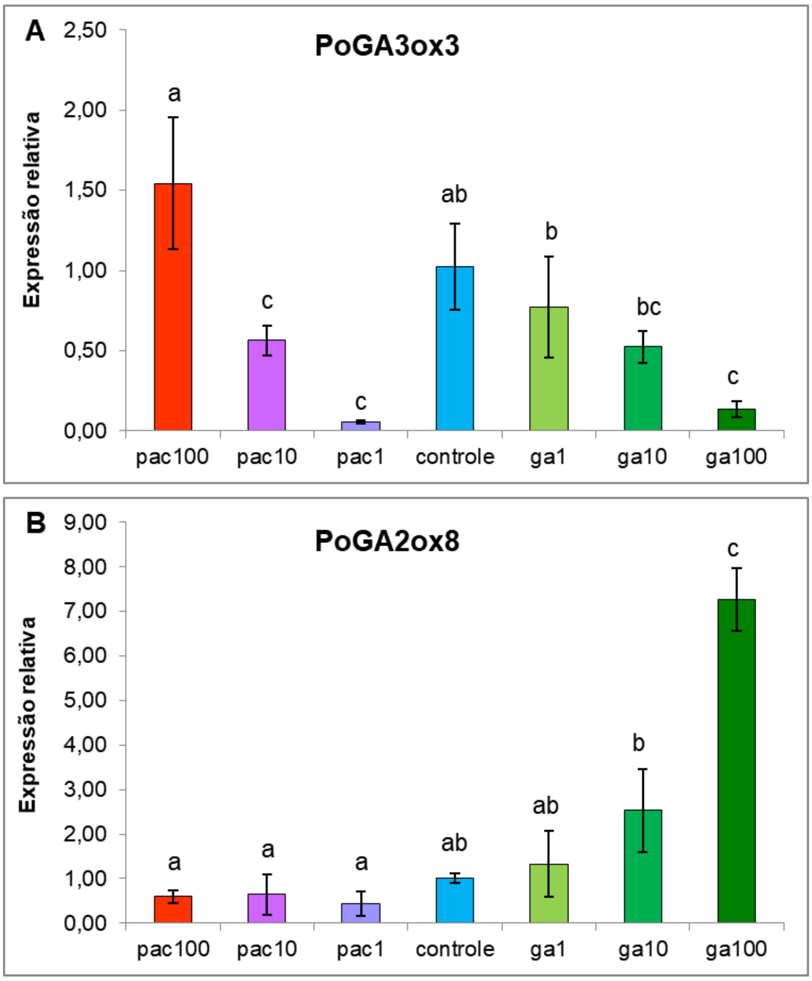

Figura 3. Expressão relativa dos genes de metabolismo de giberelina em plantas de *P. edulis* submetidas a aplicações de paclobutrazol e de GA_3. A. *PoGA3ox3*. B. *PoGA2ox8*. Os valores representam as médias ± erro padrão das três replicadas biológicas, em cada tratamento, considerando-se três replicatas técnicas. Médias que apresentam letras diferentes possuem diferença estatisticamente significante pelo teste de Tukey com 95% de significância.

A diminuição da expressão de *PoGA3ox3*, sendo um gene de biossíntese, e aumento da expressão de *PoGA2ox8*, sendo um gene de catabolismo, conforme aumentamos a concentração de GA_3 aplicado, eram resultados esperados. Isso porque os níveis de GA em um determinado tecido vegetal são determinados pelas suas taxas de biossíntese e catabolismo, que consistem na conversão de formas não bioativas em bioativas e de formas bioativas em inativas, respectivamente (Yamaguchi 2008). A regulação transcricional da biossíntese de GA já é bastante conhecida em plantas modelo: o tratamento com GAs bioativos inibe a transcrição de GA20ox e GA3ox, enquanto estimula a transcrição GA2ox, permitindo que a homeostase do GA seja mantida (Israelsson et al. 2004).

Logo, quando se aplica GA exógeno ou algum inibidor da biossíntese de GA em uma planta, ocorrem ajustes em seu metabolismo, havendo alterações das taxas metabólicas de modo a equilibrar os níveis do fitormônio (Rieu et al. 2008; Lee et al. 2020). Este comportamento é aparentemente conservado e já foi relatado em diversas espécies. Em *Vitis vinifera*, a aplicação de GA_3 em plantas na fase adulta vegetativa causou uma diminuição da expressão de *VvGA20ox3* e *VvGA3ox2*, sendo ambos genes de biossíntese de GA. No entanto, houve aumento da expressão dos genes de catabolismo de GA como *VvGA2ox*, e *VvGA2ox1*. Portanto, a aplicação de GA exógena alterou os níveis de transcrição dos genes metabólicos de GA em direção a uma diminuição no nível de GA bioativo (Jung et al. 2014). Da mesma forma, em pêssego, *Prunus persica*, o tratamento exógeno de GA_3 nos ramos ativou a expressão de todos os sete genes de catabolismo de GA identificados (Cheng et al. 2021). Em milho, *Zea mays*, após tratamento com GA, em que as expressões de *ZmGA2ox1* e *ZmGA2ox4*, foram significativamente mais elevadas, enquanto as expressões de *ZmGA20ox7*, *ZmGA3ox1* e *ZmGA3ox3* foram significativamente mais baixas que o controle (Ci et al. 2021). O mesmo comportamento foi observado em plantas de juta (*Corchorus* sp.) em que o nível de expressão do gene *CoGA3ox2*, de biossíntese de GA, foi regulado negativamente após tratamento com GA (Honi et al. 2020). Por outro lado, a GA aumentou o nível de expressão de *CoGA2ox3* e *CoGA2ox5*, de catabolismo de GA, enquanto o PAC diminuiu seu nível de expressão (Honi et al. 2020). A aplicação de inibidores da biossíntese de GA geralmente possuem efeito oposto ao da aplicação de GA exógeno na expressão desses genes, desta forma, *VvGA3oxs* e *VvGA20oxs* mostraram aumento em sua transcrição em plantas de *V. vinifera* sob tratamento com uniconazol (He et al. 2019).

Os genes *GAOXIDASES* são relatados como estando envolvidos em muitos processos importantes do desenvolvimento vegetal (Hernández-García et al. 2021). O estudo da expressão dos genes envolvidos nas vias de biossíntese e desativação de GAs ajudam a explicar em termos moleculares a ação pleiotrópica destes genes no desenvolvimento das plantas (Huang et al. 2015). Seus papéis fisiológicos podem ser observados principalmente através de mutações ou superexpressão destes genes e observações dos fenótipos resultantes. Algumas dessas alterações mais comuns foram no tamanho das plantas. Em melancia, *Citrullus lanatus*, a mutação de um GA3ox gerou plantas com fenótipo anão, sendo o fenótipo selvagem resgatado por aplicações de GA_3 ou $GA_4 + GA_7$ (Sun et al. 2020). A superexpressão do *GA2ox6* em arroz (*Oryza sativa*) diminuiu os níveis de giberelina ativa gerando plantas com fenótipo anão (Huang et al. 2010).

A regulação dos níveis de GA além de modular a arquitetura das plantas, sobretudo na fase juvenil, apresenta outros efeitos fisiológicos que podem ser interessantes principalmente para o melhoramento de plantas cultivadas. Um grande desafio da produção vegetal é a otimização da arquitetura das plantas para maior produtividade, tolerância ao estresse abiótico e maior eficiência do uso de água (Lo et al. 2017). Uma abordagem que tem sido muito utilizada é o aumento da expressão de *GA2ox*, de catabolismo de GA, para a obtenção de plantas de arquitetura mais compacta sem ser necessária a utilização de tratamentos químicos (Gargul et al. 2013).

Em estudos realizados com diferentes espécies, nos quais foram superexpressos genes *GA2ox*, houve acúmulo nos níveis de clorofila, além de alterações na morfologia foliar, gerando folhas menores e mais espessas (Gargul et al. 2013; Wuddineh et al. 2015; Lo et al. 2017; Yan et al. 2017). Em *Kalanchoë blossfeldiana* e *Petunia hybrida*, plantas ornamentais, a superexpressão de um *GA2ox* de *Nicotiana tabacum* gerou plantas mais curtas e compactas que as do tipo selvagem, embora os números médios de nós fossem semelhantes (Gargul et al. 2013). Além disso, as linhagens transgênicas de ambas as espécies exibiram alterações na morfologia foliar, tendo folhas menores, mais grossas, de coloração verde mais escura. Essas características podem ser consideradas vantajosas para a produção de plantas ornamentais. Contudo, com a superexpressão de *GA2ox*, e consequente redução dos níveis de GA endógeno, houve atraso no florescimento, e isso seria uma desvantagem para a produção (Gargul et al. 2013). Da mesma forma, a superexpressão de *GA2ox6* de *Brassica napus* em *Arabidopsis* resultou em plantas com altura reduzida e atraso no florescimento, além de aumento dos níveis de clorofila (Yan et al. 2017). Em *Panicum virgatum* a superexpressão de *PvGA2ox5* e *PvGA2ox9*, resultou em plantas com folhas verde-escuras e arquitetura modificada, mais compacta, com mais perfilhos, maior quantidade de lignina e açúcares (Wuddineh et al. 2015). Estas características são interessantes para aumentar a produtividade da espécie que é utilizada como biocombústivel, aumentando a biomassa e a qualidade do biocombústivel produzido (Wuddineh et al. 2015).

Possivelmente, as alterações morfológicas geradas com a superexpressão de genes *GA2ox* além do aumento do acúmulo de clorofila, geraram maior tolerância ao estresse hídrico e osmótico, por exemplo em batata (*Solanum tuberosum*) (Shi et al. 2019) e arroz (*Oryza sativa*) (Lo et al. 2017). Em arroz, a redução dos níveis de GA endógeno por meio da superexpressão do gene *GA2ox6* gerou plantas com altura reduzida, maior número de perfilhos (brotos), folhas com coloração verde mais escura e mais espessas (Lo et al. 2017). Além disso, as plantas transgênicas apresentavam maior tolerância à desidratação, por conta dos níveis mais elevados de clorofila, além de maior tolerância a alta salinidade e variações de temperatura (Lo et al. 2017).

A abordagem contrária, mutação de genes de biossíntese de GA para reduzir seus níveis, também tem sido realizada. Para a redução de ervas daninhas ou espécies invasoras, a diminuição dos níveis de GA endógeno mostrou-se uma estratégia interessante, que reduziria a utilização de herbicidas. Em nabo bravo (*Raphanus raphanistrum*), com a mutação de um dos *GA3ox*, mesmo diminuições leves de GA causaram reduções consideráveis no crescimento e fecundidade da planta (Groszmann et al. 2020).

Considerando tudo o que foi exposto, pode ser utilizada a abordagem de mutação ou de superexpressão dos genes de biossíntese e catabolismo de GA para acelerar ou retardar a transição para a fase adulta vegetativa em espécies de *Passiflora*. Sabe-se até o momento que o aumento dos níveis de GA acelerou a transição para a fase adulta vegetativa em *Passiflora organensis*, através de pulverizações de GA_3, enquanto aplicações de paclobutrazol reprimiram esta transição (ver Capítulo II). Portanto, esta pode ser considerada uma estratégia válida na modulação da arquitetura de plantas de maracujazeiro, visto que, a transição para a fase adulta vegetativa é quando a arquitetura do vegetal é definida (Gioppato e Dornelas 2021). E os níveis de GA, além de interferirem no crescimento da planta e na morfologia foliar (Gargul et al. 2013; Wuddineh et al. 2015), atuam sobre a plasticidade dos meristemas axiliares que possuem um grande papel na definição da estrutura da planta (Moraes et al. 2019).

Passamos agora para os genes envolvidos nas vias de sinalização de GA: Os três genes DELLA avaliados neste estudo, *PoDELLA2*, *PoDELLA3* e *PoDELLA5*, tiveram respostas similares: sua expressão foi aumentada com o aumento da concentração de GA_3 aplicada nos tratamentos, enquanto as aplicações de PAC causaram a redução na expressão desses genes (Figura 4). Para o PAC não houve efeito de dose, pois os tratamentos pac100, pac10 e pac1 não tiveram diferença significativa pelo teste de Tukey para os três genes.

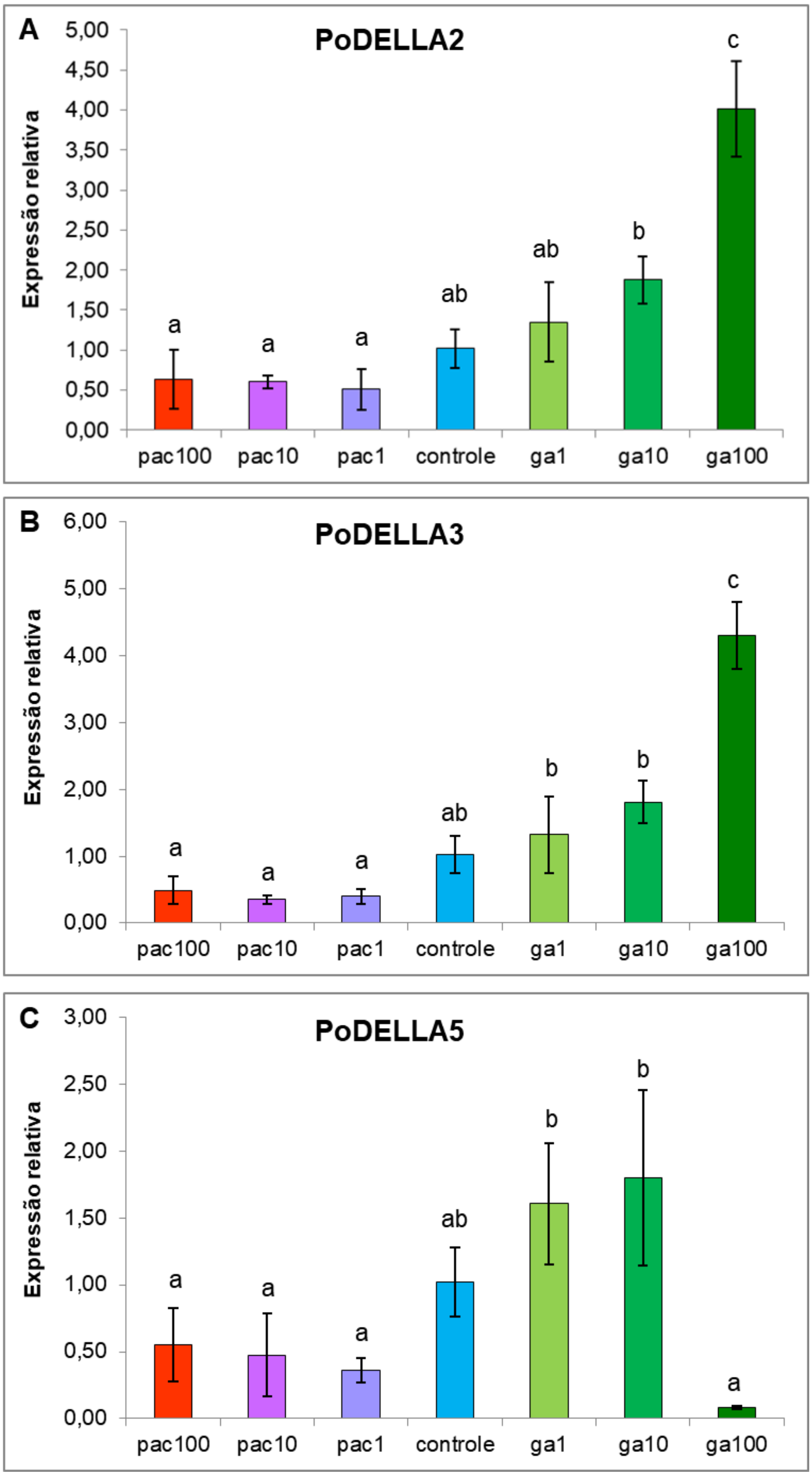

Figura 4. Expressão relativa dos genes de resposta à giberelina em plantas de *P. edulis* submetidas a aplicações de paclobutrazol e de GA_3. A. *PoDELLA2*. B. *PoDELLA3*. C. *PoDELLA5*. Os valores representam as médias ± erro padrão das três replicadas biológicas, em cada tratamento, tendo cada uma três replicatas técnicas. Médias que apresentam letras diferentes possuem diferença estatisticamente significante pelo teste de Tukey com 95% de significância.

Para os genes *PoDELLA2* (Figura 4A) e *PoDELLA3* (Figura 4B), os tratamentos ga10 e ga100 tiveram diferença estatisticamente significativa, sendo maior a expressão em ga100. Porém, em *PoDELLA5* (Figura 4C), o tratamento ga100 apresentou a menor expressão relativa, sendo até mesmo inferior à dos tratamentos com PAC. As hipóteses para este comportamento são que a dose de 100µm pode ter se tornado tóxica, causando a redução da expressão do gene; ou que pode ter provocado um efeito de repressão do *PoDELLA5*.

Os ortólogos identificados no genoma de *P. organensis* no presente trabalho foram denominados de acordo com a similaridade com as sequências proteicas de *Arabidopsis* (ver Capítulo III). Os cinco genes *DELLA* de *Arabidopsis* (Nakajima et al. 2006) possuem nomes específicos de acordo com as funções desempenhadas pelas proteínas, que já foram estabelecidas: *AtDELLA1* é denominado *GA INSENSITIVE* (*GAI*) (Peng et al. 1997), *AtDELLA2* é o *RGA-LIKE1* (*RGL1*), *AtDELLA3* é o *REPRESSOR OF GA1–3* (*RGA*) (Silverstone et al. 1998), *AtDELLA4* e *AtDELLA5* são os *RGA-LIKE2* e *3* (*RGL2* e *RGL3*) (Lee et al. 2002). Há evidências de que estes genes possuam funções diferentes embora essas funções possam ser sobrepostas (Wen e Chang 2002). *RGA* e *GAI* têm funções similares em reprimir o crescimento do caule sendo que *RGA* possui um papel dominante (Dill et al. 2001). RGL1 estaria relacionado ao desenvolvimento floral, no desenvolvimento de óvulos e anteras (Wen e Chang 2002), embora *RGL2* e *RGA* também promovam o desenvolvimento floral, de pétalas, anteras e estames (Cheng et al. 2004). *RGL2* e *RGL3* reprimem a germinação das sementes (Lee et al. 2002; Piskurewicz e Lopez-Molina 2009).

Encontramos quatro genes *DELLA* em *P. organensis*, e analisamos a expressão de apenas três: *PoDELLA2*, *PoDELLA3* e *PoDELLA5*, que seriam mais similares à *RGL1*, *RGA* e *RGL3* de *Arabidopsis*, respectivamente. Observamos que o comportamento de *PoDELLA2* e *PoDELLA3* foi mais semelhante entre si, visto que as plantas submetidas a 100µM de GA_3 tiveram expressão relativa maior e significativa desses genes em relação aos outros tratamentos. Todavia, seria necessário repetir os experimentos e realizar análises adicionais para determinar as funções desses genes e verificar se de fato correspondem aos ortólogos de *Arabidopsis* cujas funções já são conhecidas.

Em relação às funções das proteínas DELLA especificamente relacionadas à transição juvenil-adulto vegetativa, sabe-se que elas regulam o desenvolvimento dos meristemas axilares, o padrão de ramificação e o tamanho do meristema de inflorescência, através de estudos realizados com mutantes (Bassel et al. 2008; Davière et al. 2014; Serrano-Mislata et al. 2017; Zhang et al. 2020).

Um estudo realizado com mutantes quíntuplos para todos os *DELLA* de *Arabidopsis* revelou que as proteínas DELLA regulam o desenvolvimento dos meristemas axilares através da interação com a SQUAMOSA-PROMOTER BINDING PROTEIN LIKE 9 (SPL9), que reprime o expressão do LATERAL SUPPRESSOR (LAS), que por sua vez regula iniciação do meristema axilar (Zhang et al. 2020). Também foi sugerido que proteínas DELLA regulam a arquitetura das plantas por reprimirem a transcrição de TCPs (TEOSINTE BRANCHED1, CYCLOIDEA, e PROLIFERATION CELL FACTOR) de classe I no meristema de inflorescências em *Arabidopsis*, controlando a altura das plantas (Davière et al. 2014). Os TCPs por sua vez, estão relacionados ao crescimento da planta pela proliferação de células meristemáticas (Martín-Trillo e Cubas 2010). Em tomateiro (*Solanum lycopersicum*) há apenas um gene que codifica uma proteína DELLA, o *PROCERA* (Bassel et al. 2004). A mutação deste gene altera a arquitetura do tomateiro, modificando seu padrão de ramificação, por meio de supressão diferencial do desenvolvimento dos meristemas axilares, e isso indica um papel para as proteínas DELLA na regulação da estrutura dos vegetais (Bassel et al. 2008). Considerando que os genes *DELLA* podem apresentar papéis diversos relacionados à transição da fase juvenil para a adulta vegetativa, seriam interessantes análises adicionais para determinar possíveis funções, inclusive verificando suas expressões em diferentes tecidos, para assim, posteriormente, obter características de interesse nas plantas de *Passiflora*, através da modulação desses genes.

Conclusões

A aplicação de giberelina exógena induziu alterações nos padrões de expressão dos genes relacionados à biossíntese, catabolismo e resposta à giberelina em plantas juvenis de *Passiflora edulis*. Conforme o aumento na concentração de giberelina aplicada, o gene *PoGA3ox3* teve uma diminuição gradual em sua expressão, enquanto o *PoGA2ox8* e os *PoDELLA2*, *PoDELLA3* e *PoDELLA5* tiveram aumento. O paclobutrazol causou efeito oposto ao da GA_3, como era esperado, apesar de não ter sido observado efeito de dose nos experimentos realizados.

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DISCUSSÃO GERAL

Os fitormônios são importantes fatores que influenciam no estabelecimento da arquitetura da planta, destacando-se os papeis de citocininas e giberelinas. Estes, agem de maneira antagônica. Seu balanço define basicamente a quantidade de ramos formados, altura da planta e momento em que ocorre a transição da fase juvenil para a adulta vegetativa (Gioppato e Dornelas, 2021).

Os papeis destas classes de fitormônios é evidenciado por sua influência na formação de estruturas vegetativas ou reprodutivas a partir de meristemas indiferenciados, sendo que as giberelinas estimulam esta transição de fases, através da formação de gavinhas (que são inflorescências modificadas), enquanto as citocininas estimulam a formação de ramos vegetativos, durante a fase juvenil.

A compreensão da ação de citocininas e giberelinas na transição da fase juvenil para a adulta vegetativa pode permitir a manipulação das características das plantas para a obtenção de características de interesse (Barbosa e Dornelas, 2021). Os resultados que obtivemos com *Passiflora organensis* e *P. edulis* podem ser aplicados a outras espécies, principalmente frutíferas, embora sejam necessários estudos adicionais.

O aumento da concentração dos fitormônios nas plantas pode ser realizado principalmente por duas abordagens: por aplicações dos fitormônios diretamente sobre as plantas através de spray, para que sejam absorvidos principalmente pelas folhas (Jung et al. 2014); ou através da produção de plantas transgênicas, de forma que possam expressar menos ou mais os genes relacionados ao metabolismo dos hormônios desejados (neste caso, citocininas e giberelinas). Para esta segunda abordagem, faz-se necessário o conhecimento da expressão destes genes, relacionados ao metabolismo destes genes e do comportamento destes genes quando a planta é submetida a aumento da concentração dos fitormônios exógenos.

A caracterização das famílias gênicas que codificam as enzimas de metabolismo e resposta a citocininas e giberelinas podem fornecer a base para uma melhor compreensão de como esses hormônios atuam no desenvolvimento de espécies de *Passiflora*. Obtivemos as sequências genômicas de genes relacionados ao metabolismo e à resposta a citocininas e giberelinas, e as sequências proteicas, que podem ser utilizadas como base para futuros estudos.

CONCLUSÕES GERAIS

A transição da fase juvenil para a adulta vegetativa nos vegetais em geral ainda necessita de informações sobre suas alterações moleculares, tendo em vista sua importância, e a possibilidade de moldar as características estruturais dos vegetais durante este estágio.

Neste trabalho, observamos que aplicações de giberelina induziram a diminuição na expressão de um dos genes de síntese de GA de *Passiflora organensis* em plantas de *P. edulis*, *PoGA3ox3,* e aumento de expressão de um dos genes de catabolismo de GA, *PoGA2ox8*. Isto seria necessário para a regulação da concentração da GA. Os genes que codificam proteínas DELLA tiveram aumento na expressão quanto maior foi a concentração de GA aplicada. Como as DELLA regulam negativamente a ação da GA, este comportamento era também esperado. Contudo, algumas anomalias foram observadas, pois passou-se muito tempo desde a aplicação dos fitormônios até as análises de expressão gênica. Um outro fator que pode ter influenciado a qualidade das amostras foi a questão da especificidade dos primers. Projetamos os experimentos para serem realizados com plantas de *Passiflora organensis*. Porém, as plantas de *P. organensis* que utilizamos para as análises morfológicas foram obtidas a partir de propagação vegetativa e não a partir de sementes. Por isso, estas eram mais difíceis de obter. Nossa ideia inicial era repetir os experimentos com *P. organensis* e analisar a expressão dos genes relacionados ao metabolismo e resposta a citocininas também. Contudo, não foi possível repetir os experimentos, devido à pandemia da COVID-19.

Em suma, nosso estudo fornece informações sobre como ocorre a transição da fase juvenil para a adulta vegetativa em *Passiflora*, contribuindo para a compreensão do desenvolvimento vegetal. Esperamos que estes estudos possam igualmente subsidiar estudos futuros de modulação fisiológica da arquitetura de plantas de maracujá e indiquem caminhos para o melhoramento genético visando a obtenção de variedades comerciais de maracujá com arquitetura de planta alterada.

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APÊNDICE A – GENES ENVOLVIDOS NO METABOLISMO E RESPOSTA A CITOCICNINAS E GIBERELINAS

Tabela 1. Genes envolvidos no metabolismo e resposta a citocininas, de *Arabidopsis thaliana, Passiflora organensis* e *Vitis vinifera*, com os respectivos números de acesso no NCBI

Síntese de CK			
IPT	*Arabidopsis thaliana*	AtIPT1	AEE347961
		AtIPT2	BAB590421
		AtIPT3	AEE804361
		AtIPT4	AEE849381
		AtIPT5	ANM705571
		AtIPT6	AEE306191
		AtIPT7	AEE767881
		AtIPT8	BAB590471
		AtIPT9	AED927841
	Vitis vinífera	VvIPT1	XM_002279335
		VvIPT2	XM_002263711
		VvIPT3a	XM_002268812
		VvIPT3b	XM_002271926
		VvIPT5a	XM_003632592
		VvIPT5b	XM_002277555
		VvIPT9	XM_002282976
	Passiflora organensis	PoIPT1a	
		PoIPT1b	
		PoIPT2	
		PoIPT3a	
		PoIPT3b	
		PoIPT5a	
		PoIPT5b	
		PoIPT7a	

		PoIPT7b	
		PoIPT7c	
LOG	*Arabidopsis thaliana*	AtLOG1	At2g28305
		AtLOG2	At2g35990
		AtLOG3	At2g37210
		AtLOG4	At3g53450
		AtLOG5	At4g35190
		AtLOG6	At5g03270
		AtLOG7	At5g06300
		AtLOG8	At5g11950
		AtLOG9	At5g26140
	Vitis vinífera	VvLOG1a	XP_0022852461
		VvLOG1b	XP_0022778521
		VvLOG3	XP_0022762792
		VvLOG5a	XP_0106640901
		VvLOG5b	XP_0022818391
		VvLOG7	XP_0022754141
		VvLOG8a	XP_0022857162
		VvLOG8b	XP_0022783051
		VvLOG10a	XP_0022767751
		VvLOG10b	XP_0022747471
	Passiflora organensis	PoLOG1a	
		PoLOG1b	
		PoLOG2	
		PoLOG3a	
		PoLOG3b	
		PoLOG5a	
		PoLOG5b	
		PoLOG7a	
		PoLOG7b	
		PoLOG7c	
Degradação de CK			

CKX	*Arabidopsis thaliana*	AtCKX1	AEC099921
		AtCKX2	AEC068891
		AtCKX3	AED968281
		AtCKX4	AEE856691
		AtCKX5	AEE357211
		AtCKX6	AEE804821
		AtCKX7	Q9FUJ11
	Vitis vinifera	VvCKX1	AXP073681
		VvCKX3a	AXP073691
		VvCKX3b	AXP073701
		VvCKX3c	AXP073711
		VvCKX5	AXP073751
		VvCKX6	AXP073761
		VvCKX7	AXP073771
	Passiflora organensis	PoCKX1a	
		PoCKX1b	
		PoCKX3a	
		PoCKX3b	
		PoCKX5	
		PoCKX6a	
		PoCKX6b	
		PoCKX7a	
		PoCKX7b	
Resposta a CK			
ARRs tipo A	*Arabidopsis thaliana*	ARR3	AT1G599401
		ARR4	AT1G104701
		ARR5	AT3G481001
		ARR6	AT5G629201
		ARR7	AT1G190501
		ARR8	AT2G413101
		ARR9	AT3G570401
		ARR15	AT1G748901

		ARR16	AT2G406702
		ARR17	AT3G563801
	Vitis vinífera	VvRR3	CAO409691
		VvRR4	CAO42848
		VvRR5	CBI150983
		VvRR9a	CAO428481
		VvRR9b	CAO630611
		VvRR9c	CBI401593
		VvRR17	CAO415171
	Passiflora organensis	PoRR3	
		PoRR4	
		PoRR5	
		PoRR6	
		PoRR8	
		PoRR9	
		PoRR16a	
		PoRR16b	
		PoRR17a	
		PoRR17b	
ARRs tipo B	*Arabidopsis thaliana*	ARR1	At3g16857
		ARR2	At4g16110
		ARR10	At4g31920
		ARR11	At1g67710
		ARR12	At2g25180
		ARR13	At2g27070
		ARR14	At2g01760
		ARR18	At5g58080
		ARR19	At1g49190
		ARR20	At3g62670
		ARR21	At5g07210
	Vitis vinífera	VvRR1	RVW399571
		VvRR2	CBI369113
		VvRR10	CBI181313

		VvRR11a	CBI269613
		VvRR11b	CAO466981
		VvRR12	CBI210843
	Passiflora organensis	PoRR1	
		PoRR2	
		PoRR10	
		PoRR11a	
		PoRR11b	
		PoRR12	
		PoRR13	
		PoRR14	
		PoRR18a	
		PoRR18b	
		PoRR21	

Tabela 2 Genes envolvidos no metabolismo e resposta a giberelinas, de *Arabidopsis thaliana*, *Passiflora organensis* e *Vitis vinifera*, com os respectivos números de acesso no NCBI

Síntese de GA			
GA3oxidase	*Arabidopsis thaliana*	AtGA3ox1	NP_1730081
		AtGA3ox2	NP_1781501
		AtGA3ox3	NP_1939001
		AtGA3ox4	NP_1781491
	Vitis vinífera	VvGA3ox1	AGQ426111
		VvGA3ox2	AGQ426101
		VvGA3ox3	AGQ426121
	Passiflora organensis	PoGA3ox1a	
		PoGA3ox1b	
		PoGA3ox2	
		PoGA3ox3	
GA20-oxidase	*Arabidopsis thaliana*	AtGA20ox1	NP_194272
		AtGA20ox2	NP_199994
		AtGA20ox3	NP_196337
		AtGA20ox4	NP_176294
		AtGA20ox5	NP_175075
	Vitis vinífera	VvGA20ox1	CBI244703
		VvGA20ox2	CBI388183
		VvGA20ox3	CBI375103
		VvGA20ox4	CBI189503
		VvGA20ox5	CBI375213
	Passiflora organensis	PoGA20ox1a	
		PoGA20ox1b	
		PoGA20ox2a	
		PoGA20ox2b	
		PoGA20ox3	
		PoGA20ox5	

Degradação de GA			
GA2oxidase	*Arabidopsis thaliana*	AtGA2ox1	NP_1779651
		AtGA2ox2	NP_1742961
		AtGA2ox3	NP_1810021
		AtGA2ox4	NP_1752331
		AtGA2ox6	NP_1717421
		AtGA2ox7	NP_1755091
		AtGA2ox8	NP_1938522
	Vitis vinifera	VvGA2ox1	CBI308873
		VvGA2ox2	CBI330243
		VvGA2ox3	CBI330233
		VvGA2ox4	CBI228443
		VvGA2ox6	CBI369903
		VvGA2ox7a	CBI239323
		VvGA2ox7b	CBI274763
		VvGA2ox7c	CBI239313
	Passiflora organensis	PoGA2ox1a	
		PoGA2ox1b	
		PoGA2ox4a	
		PoGA2ox4b	
		PoGA2ox6a	
		PoGA2ox6b	
		PoGA2ox7	
		PoGA2ox8	
Sinalização de GA			
DELLA	*Arabidopsis thaliana*	AtDELLA1	NP_1729451
		AtDELLA2	NP_1768091
		AtDELLA3	NP_1782661
		AtDELLA4	AEE739451
		AtDELLA5	AAO648401
	Vitis vinífera	VvDELLA1	KY765590
		VvDELLA2	KY765592

		VvDELLA3	KY765594
	Passiflora organensis	PoDELLA1	
		PoDELLA2a	
		PoDELLA2b	
		PoDELLA3	
Resposta a GA			
GID1	*Arabidopsis thaliana*	AtGID1a	At3g05120
		AtGID1b	At3g63010
		AtGID1c	At5g27320
	Vitis vinífera	VvGID1a	KY765590
		VvGID1b	KY765592
	Passiflora organensis	PoGID1a	
		PoGID1b	
		PoGID1c	

APÊNDICE B – SEQUÊNCIAS DOS PRIMERS DOS GENES DO METABOLISMO E RESPOSTA A GIBERELINAS

Tabela 1. Sequências dos primers dos genes do metabolismo e resposta a giberelinas (obtidos a partir das sequências de *Passiflora organensis*) que não foram utilizados nas qRT-PCRs realizadas neste estudo.

Gene	Tipo	Sequência do primer	Tamanho do transcrito (pb)
PoGID1aF1	Fw	GGCTTATGTTGAAGGGCTGA	184
PoGID1aR1	Rw	AGTATGGCTGCCAGTCAGGT	
PoGID1b1F1	Fw	AAGGGCTCGAGAAAGCTGAT	200
PoGID1b1R1	Rw	CGATCCAAGTGAGAAGGTCA	
PoGID1b2F1	Fw	CAGGCCACGATAGGGTTCTA	131
PoGID1b2R1	Rw	TGTCATGTACGGAAGCCTGT	
PoDELLA1F1	Fw	TCCGGTGGTGAAGGGTATAG	100
PoDELLA1R2	Rw	CCCACTAGAAAGGTTAATTA	
PoGA2ox2F1	Fw	ACTGCCACCAAGAAATCACC	178
PoGA2ox2R1	Rw	GCCTGTAATCAGCCAGCTTT	
PoGA2ox3F1	Fw	TGGCAATCAAAGGAGAGGAG	107
PoGA2ox3R1	Rw	CTCAAACATTCCGAGCCTGT	
PoGA2ox4aF1	Fw	CAAGGATCAGTGCTCCATCA	109
PoGA2ox4aR1	Rw	TCCCCAAGCCGTAAAGAGTA	
PoGA2ox4bF1	Fw	AGCGCTCCAGCTGATATTGT	193
PoGA2ox4bR1	Rw	TCCCACCGTCAGCTACTTTT	
PoGA2ox6aF1	Fw	TGGATCTCTCCTCTCCCTGA	192
PoGA2ox6aR1	Rw	TCTTTTCCGAGTCTGGCTTC	
PoGA2ox6bF1	Fw	CGGATATCTCCTCACCCAGA	116
PoGA2ox6bR1	Rw	AGACGGGTGTCCCCTAATCT	
PoGA2ox7F1	Fw	TGCAGAAAGCCTGCAGTGTA	108
PoGA2ox7R1	Rw	CAGGAACCTGGAGAGTCCAA	
PoGA2ox6aF2	Fw	AGGATTTGTGACAAGTGATC	100
PoGA2ox6aR2	Rw	TTAAAATATACATCTTCAAT	

PoGA3ox1F1	Fw	TATCATGCGTGAGAGTGTGC	100
PoGA3ox1R1	Rw	GAGGCTGTTCCTGTCTGGTC	
PoGA3ox2F1	Fw	GGCCACCATCATGTGTTAAG	192
PoGA3ox2R1	Rw	TAGCTAGCCATCAGCCAACC	
PoGA3ox5F1	Fw	GGTTGTCCGTGGCATATTTC	103
PoGA3ox5R1	Rw	CCCACGGATATTGAACGGTA	
PoGA20ox1F1	Fw	TCACGCAGAAGCATTACAGG	138
PoGA20ox1R1	Rw	AATAGCTCTGCCCCAGGTCT	
PoGA20ox2F1	Fw	TAACTCCCCCGACTGAACTG	148
PoGA20ox2R1	Rw	GCTGACTTTTGGAGCCAATC	
PoGA20ox3F1	Fw	AGACGTTGAGGCTGAGGAAG	102
PoGA20ox3R1	Rw	CATACGCTTGGCCCTACTTG	
PoGA20ox4F1	Fw	GTGGCGACGACTGCTAGAAT	101
PoGA20ox4R1	Rw	ACATCTGAGCCGTTGGTTGT	
PoGA20ox5F1	Fw	AGAAGGGCCAAGGAAATACC	107
PoGA20ox5R1	Rw	GCCAGTGAATGAAGCTTTGC	
PoGA20ox2F2	Fw	AAGTCAGCTGAATAAGTGAT	100
PoGA20ox2R2	Rw	GTCAATGTCACTTTCCGAGG	
PoGA20ox5F2	Fw	TCTAACCTATACTTGCCTTC	100
PoGA20ox5R2	Rw	CAATTCCACGTAACATTATC	

APÊNDICE C – SEQUÊNCIAS GENÔMICAS DOS GENES

Legenda:

Códon de início:	**ATG**
Éxon:	NNNNNNNN
Final do éxon:	**G**
Íntron:	NNNNNNNN
Começo do éxon:	**G**
Códon STOP:	**TGA** ou **TAA** ou **TAG**

Sequências genômicas dos genes relacionados ao metabolismo e resposta a citocininas em formato fasta:

> c2900 **PoIPT_2 – Biblioteca LIB15043**

ATGAAGTGCAGCAGTAGTCAGCAAGAACCCGAGCAAAGCCCTAGCGATGGAGGTGAAGGAC
TAGCAACAGAAGCCGCGAAGAAGCAAGAAGAGCGGGAAAAGAAGGCGAAGGTGGTGGTGA
TAATGGGTCCTACTGGTTCAGGAAAATCGAAATTGGCCATTGATTTGGCCGCCCACTTCCCTGT
CGAGGTCATTAACGCCGATTCAATGCAGGTCTACCGTGGCCTCGATATTCTCACCAACAAAGT
CCCCCTCCATGATCAAAAG**G**GTAATTTCTCCTTGTTGTTTCTTGGTTCTGCAATGGCTAGCTTTATGTT
CTAGTGGAGGTTTTATAATTATTAATTAGTAATGACTGTTACCGTGTGTCGTAGCCGGTAAAGTCGTTTTTT
ATGCCTGTTAGATGTTTGTTTGTTATTTTTTTACACGATTTTGTACTGTCGGATTTCTGTTGCAG**G**AGTGC
CGCATCATCTGTTGGGGACTGTTAGCCCAAATGTGGAATTCACAGCTAAGGAGTTCCGGGATT
CGGCTATTCT**T**GTAAGTTACTCTTGTATTCAGAGATTGCAAATTATGGCATGGTATGGTATGCTCGCTTGC
TTCTTGTATGTTAGTTATTGAGCGGCACTGATTTTTTATGATTTCAACTAGTCGTATGTTTTGACTTGGTCG
AGTTAATTGTTTTTCAG**C**TCATCGATGAAATATTTTCTCGGAACTGCCTGCCAGTTATTGTTGGGG
GCACGAATTACTATATTCA**G**GTAGGAGATTTTTGAATTATTTTCTTAAATTTTGCAGCACTGATAACCCA
AACTTCGATTTACAGCGTTTACTGGATGAGAACATTGAGTTGTAGATTTTGTTGCAGCTCGATCTCTCCGA
CCTTGAAAATATCAAATTATTTGGTTTTTCCCACAAATTTCATAATTCTTCAGTTTATTTGTTTTGTACCATA
GTCGATTGAGATTGTTCAAAATCTCTGCAGTCTCATGTGAAGAAATGTTTTTCTTCCTTGGCAGATAAGTT
TCTAGGTATAATAAGAAGAGTGTTGTCTCTTTTAATGCTGAGTGTTGCAACTTGTTAACTCTACTCTTCATG
TTAGTACCCCAATATTATTTTGTTCCTTTACTTGTTCAG**G**CTCTTGTGAGCTCTTTTCTCCTCGATGAT
ACTGCACAAGATCTGGATGAATGTCTTTCTTGCAATTTTCCT**G**GTAAGCAGTAAACTCGTTGCCTT
GTAATATGCATTTATAGTTTAAATCATTAGTACAGTCATTGCATTTTTGTAG**G**AGATGACCAGGCTGTGC
ACTTGCTTGAAAGCAAGACAGACACATTTGATTTTACCTATGAATTTCTCAAAAACATTGATCC
TGACGCTGCAAACAGACTCCATCCCAACAATCACAGAAA**A**GTAAGGATTTAAATATATGCTTTGAT
TTTTATTATCTCCTTTGACTTGGTGATCTGTGATGGTTATATAATATGTCTTGGAATTTCTGTTTATATCTTCG
TCTTTGATTGCTAATGAAATAGTTTACAGTTGTGAAACCTTCCATAAAAATATGTGTACAAACTGGGAAAA
TTGTGAACTCTGAATTAATCACTGAATATTGCATCTCCTTGATCTCAGATGCCTTGAGTTACTTCTTTTTAA
AAAATTAGCCTTGAGTTACTTGGCTAGGTATCTTAACAGTCTAGAAGGAATTCCCTACATTTTGCTGCCTT
ATTCAAGTTGTAAAGACTAAGATTGCTTTACTCCTCTTTGGATTTGATTGATTTTGGAAAATCTGCTGGCTT
TTGGTTTTGACATTTTTATATTTCGAAGAAAAAATGTAGTTTGACCTTTAGGTTTACCTATCCTAATAGTTTT
ATAATTAGGTTACAGAATGTTGTTTCTAGTTCTTGTGAATATGAATCCCTTGAGTCTGATATTTGTAAATAAT
GTTTTCAGGGATTTATAACCCTGCAGTTTTACAATGAAAGTTATGATGTCCTATATTTGTTTAAATCATGTG
AATATCAATGAGGACATCAGATAATAGGATTGTAAAACATCTCATATTTTTCTTGTGTGGCATCTTTGCAAG
TTGCTATTCGTGGAATTTTTCCATAAAAAGTTTAAGTTTTATGCAAAAAACCGAAAAAAGATAAAGAGAA
TAATGAATTTGGAACTTCCTTTTTGCAG**A**TTAAGCAATACCTTCATCTATATGCTCGTACTGGTATTA
TACCAAGTAAACTTTATCAGGGAAAGGCTGCACA**G**GTGGGTATTCTATCCTCTAGTAGATTGCATTT
TTATTTATTTCTAAACTTTTCTTTCAAGAATGGAGATCTTTCCTTCAATGAGTCTGATTGTCTAATTCTTATG
AATTTTACTGTGTTTTGGGTAAATTATGCATCGACTTGCAGAGCCACTAATTATTGCATTTATGGTCTTTACT
CTTTAATGGGAAATTATCTTCTTTTATGATATTTGACTCCTGCAACTCATTTTTTTATTTTTTACTTTATGAAA
TCTCTTACTATTTCCAGTGACCGTAATTTTTATTTTGAAAAATTTCACTCAGAAAAAAATGCTGTCATTAAT
CTAACATCTCAATCTGGCAGGGCAG**A**ACTGGGGTTGCATTGGTAATTGTAGATTCAATTGCTGTTT
TATATGTGTTGATGCTGCTATTCCCGTAATAGACCAGTTTGTGGACAAAAGGGTGGATTGCATG

ATAAATGCTGGATTACTTAGCGAAGTTTATGACATTTATAATATGGATGCCGATTACACTCGAGG
TCTTCGGCAAGCCATTGGTGTACGAGAATTTGATGAATTTCTGAAAGTTTGTCAATTGGCGAG
CAAGGATGATTATGCACGTGACTTGATTGGTAGTTTAAACAAGGACAAGAAGATACTGAAAGA
TCACATAAGTGCAATCCTCCATTTCACGGATGATAATCAACTCAAAATTTTGTTAACAGAAGCC
ATTGAAAAAGTAAAAGTAAATACTCGACGACTTGTTCGCCTTCA**A**GTAAGTTTTTATTTGTGTATG
TTTACATTTTTTATAAATGTTGCAATACCTATATTAACACTCAACAACCCATTCGTGGGGATTGATAAATGTT
CAGCTTCCTTAAATAATGGCCTCAAAGTTTAATTTTTGGTTATTATGTTTACTTGTATGCAAATCTCTGCTCC
ATCAGTTAGCTCATACAAAGTGACTTTACTGAACTAAACAATGATTCCCGTTATGCATGTTATTTATCCCCT
CAGATGGTTTCTGGGAAACTCAGCAACAATATGATGCATAGGTCAGTTCATTGTAGAACGAACTCATGTG
ACTTCTCATGTTGTGTTTATCTGTCACTGGGGTGAAGCTCTTCTAATTTAATGCAAACAGTTAGAAACTCT
GTACTCATGATTGTTAATGTACGGTGCTGATTACTTCCATGCATGAAATCGGCACTAATGTCTGGTGTTTAA
AATTTGGCTATAAATGTGACAGCTTTCTTACTTCTATTTCTATTTGGCAG**A**AGAGAAGGCTTAATCGGC
TTCAGACATTGTTTGGATGGAACATGCATCATCTTGATGCTACTGATCCCATTTCA**T**GTGCGCAT
TTCATATTCTCTTCTTTGAACGAAATATTTTTTCTGGCACTGCAAAGATTCTTTTGTAATCACATGGATACTA
TATTCCAG**G**CAAGTCAGATGATTCCTGGGCTACGCAAGTTGTTACCCCAGCTGCGAAAATCATC
AAATCTTTTCTAAACGAGGACAGGAGCTCGGAGGTTGAGCAGGAGGTGCACGTTGATATTGG
AACAGAATTACATGAAAGGAACCTGTGGACTCAATACACATGCAA**A**GTATGCTTGGTTTTTTCTT
TTTCTATTTCCTTTTGCTGTGTTGATTTACTGGCTCTTTTGGTGAAGATCTTAACTACAAATTTCGCTTGATT
TACAACATTTTTTTTTGCAG**G**CCTGTGGAGATAAGGTGCTTAGAGGAGCTCATGAGTGGGAACAG
CACAAACAGGGTCGTGGGCATCGAAAAAGAATTTCTCGAATTCGGAAATCAGGAAGACAAC
GCACTCTCGTAGCTGCTCAGGGTCCAGAAGCATCATCC**TGA**

> c677 **PoIPT_3A – Biblioteca LIB15043**

ATGAGCCTTTCCATGTCTGTGTGCCCACAAACAAGAAATATGCTGGATATTCTTCCTACAGCC
AGGCTCAAAATGGACATTCTGGGTCCAAGGTGGCGAAAAGACAAGGTTGTGGTCATAATGGG
AGCAACCGGTACGGGCAAGTCCCGACTCTCGATTGACATTGCAACCCGATTCCCGTCGGAAA
TCATTAACTCGGACAAAATGCAAGCTTATAAGGGCCTTAACATAGTCACCAACAAAATCACTG
AAGAAGAGATGTCCGGGGTCCCTCACCATTTGCTAGGCGTAGTGAATTCTAACTCAGAGTTCT
CTGCTACCGATTTCTGTGACATGACTTCACTGGCTGTTGAATCAATTTTGACTCGAGGCTTGCT
TCCGATCATCGTTGGTGGCTCAAATTCCTACATCGACGCTTTGATGGATGGTGGGGAGTACAG
ATTCCGATCAAAATATGACTGTTGCTTTCTCTGGATGGATGTGTCGATGCCTGTACTACACGAA
TTCGCATGCAGGCGAGTTGAACAAATGGTTAGGAATGGAATGGTTGATGAGGTGAGAAACAT
GTTTGATCCCTCCGCAGACTATACGCATGGGATCAGGAAATCAATTGGGGTCCCTGAGCTCGA
CAGGTACTTCAGAGCTGAACCGTTTTTGGATGAAGAAACCAGCGCCGGACTGCTTCATGAAG
CAATATCTGAAATCAAAAACAACACATGCATTTTAGCTTGCCGTCAACTGGAGAAAATCCATC
GGTTTATAAACATAAAAGGGTGGAATATACATCGAATTGATGCCACGGAGGTGTTCACTAGGA
ACGGAAAGGAAGCGGATGAAGCGTGGGAGAAGCTAGTGGCCAGACCCAGTTCTGCAATTGT
TGCAGAGTATCTTTACTATTCTACTGCTCAGGTCCCAGCTACTGTCGGAACTACTAAAGATTAC
TATGCGCAATGCCTTGTGGCA**TAA**

> c3062 **PoIPT_3B - Biblioteca LIB15043**

ATGAACCTTGCTATGTCTCTCTGCCAACAAACAAGTAATGTGCTCGACATTCCCGGCGGAAGA
CTGAAAATGGACATTCTAGGCCCGAGGTGGCAAAAGGACAAGGTGGTTGTCTTAATGGGAGC
AACTGGAACAGGCAAGACTCGACTCTCTATCGACATTGCAACCCAGTTCCCATCAGAAATCAT
CAACTCCGACAAAATGCAAGCTTACAGGGGCCTTGACATAGTCACCAACAAAATCAGTAAAC
AAGAGATGAGCGGGATCCCTCACCATTTGCTAGGCATAAGGAATCCTAATTCAGAATTTACAG
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AATCATCGTTGGAGGTTCCAATTCCTACGTCGAGGCTCTGATGGATGGTGGTCAGTACAGATT
CCGTTCAAAATACGACTGCTGCTTCCTCTGGGTGGATGTATCTGTTCCTGTGCTTCACGAATCT
CTACGCAAGAGGGTTGATCAAATGGTTGGTAATGGAATGGTCGATGAGGTGAGGAACCTATTC
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GAGAGGAAGCGGAAAAGACATGGGAAAAGCTTGGGTCCAAACCCAGTTCTGCAATTGTTCG

ACAGTTCCTATACAACATTATTAACAAGGTCCCAGCAACTGCAGCAAGTGCTAAGGATTACTT
TGAACATTGCCTTGTCGCA**TAA**

> c1513 **PoIPT_5 - Biblioteca LIB15043**

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GCTCTGAACAAGAACCCCTTCCATTGTCGCAAAGACAAGATTGTGTTTGTGATTGGACCCACA
GGCACGGGCAAGTCGAGAGTAGCTATTGACATGGCAACTCGAATTCCGGCGGAGATTGTCAA
TTGTGACAAAATGCAAGTTTTTAAAGGCCTTGACATAGTAACAAACAAAGTCACCGAAGAGG
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GGACTTTAGGATTCATGCATCCCTGGTGCTTGAATCAATTGTGGCGCGCGATCGGCTGCCTATA
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GTTGATCGGATGGTGGAAGCGGGCTTGATCGACGAGGTCAGGAATATGTTTGATCGGAATAGG
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TAAAGAAAACACTTGCATTCTAGCTTGTCGTCAACTACAGAAGATCCATCGCCTTCGTAGCCG
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CAGATGAAGCATGGGAGAAACTTGTTGCAGGACCCAGTACAATGATCCTGAATAAATTCCTGT
ACGACACCGTTTCACCATCGGAATCCGTGGACATCCCAATCATTGGCCCTGCAGTGCCACTCC
CCATACCTGCCATGGCAGCAGCAGCAGCAGCATCTAGG**TAG**

> c1471 **PoIPT_6 - Biblioteca LIB15043**

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CGCTTCCCTTCCGAAATCATCAACTCCGATAAAATGCAAGTTTATAATGGTCTCGACTTGACAA
CCAACAAAGTCCCGCCACATGAACGCCACGGAATCCCGCACCATTTGTTTGGCGAGGTTGAC
CCGGACGAGGGCGAGTTCTCCCCCTTCGATTTCCGGGTGGCAGGTGGGTTGGCTGTGTCAGA
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GTGGTTGACCGGTTTACCCCCGCGTCGGACGTGTTCTACGGGTTGGACCCGGTTTCTCCCCAG
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GTCCGGCGAGTCGGCGAATCAGCCCGGGTTGAGGAAGGCGATCGGGGTGCCCGAGTTCGAG
AAATATTTTAACAAGTACGGGCCAGGGTGTGACCGAAGGAAGTGGGATCGTTTGCGGACGGA
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ATATTCAGACAGTCGATGATGATGATGACGACGACGTCACCGTCGGAGGATTACTGTCACCGC
GACAGCGGCAACCGCAAAGAAGAATGGCTACCGGAGGAAAAATGGAGGAGGAAGAAGAAG
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GTTTTCTGGAGGAG**TAG**

> c151 **PoIPT_7 - Biblioteca LIB15043**

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TCAGGACTAATGCATCTCTGGTGCTTGAATCAATCGTGGCACGCAATCGACTACCAGTCATCG
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> c1815 **PoIPT_8 - Biblioteca LIB15043**

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GGGGGTCCGTATGGACTCCTCCGCCTCCCACCGCTTGAAAGAGAAGGTTGTTGTCATAATAGG
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CACCCCTTCCGAGTTCCGGGTAGCGGGCGGGTTGGCTGTGTCGGATATTGTTTCAAGGAAAA
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TCAGCCCGGGTTAAGGAAGGCAATTGGGGTGCCCGAGTTCGGGCAATATTTTAGGAAATACG
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ACGAGAGATTAAAGAAAACACGTGTCAGCTAGCGAAGAGGCAGATAGGGAAGATCATGAAA
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AGAAGAAGAAGAAGCAGAAGAGATGCAGTAAGAAGAAGAAGAGGTGGATGGAATTGGTTT
GGGAGAGAGAAGTTTTGGAGCCAAGCGTGAAGATTGTGAAGCGTTTTTTGGAGGAG**TAG**

> c17929 **PoIPT_9 - Biblioteca LIB15043**

ATGCCAGTTGGTGGGTCACCTGTCCCTACGAGGAAGAAAATGATGAGCATTCAGAGGCTTC
GAGTTCAGTATAATTCTACTT**C**GTAAGTACACTTTTTGATCCAGGTCAGAAAAAATTAAAGAAAAG
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ACCATTTTACTTTGCCACAG**T**ACTGACATTAATGCAAACACAAACGTTATCAAACAAGACACCG
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GATTTGGCCACCCATTTGAACGGGGAAATCATCAGTGCAGATAAAATTCAGGTGTACAGGG
GGCTCGACATAGCAAGCAACAAAATCACCGAAAATGATCAAGGGGGCGTGCCCCACTATTT
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TGC**TGA**

>c715 **PoLOG_1 - Biblioteca LIB15042**

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TGGAGGAGGAAGTATTGGTTTGATGGGTCTGATCTCACAAGCTGTTTATGATGGCGGCCGCC
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GAACTATCTCATTCTCTTGTTAGTTCCCATTTTGTGATCTCTGTTTCAACCATCCAGATTAAGGAAAACC
CAACTTTGAGCTATAAAAATGGTTGTTTCTTCCTGGAAG**G**TGGGATTGCTGAATGTGGATGGCTAT
TACAACTCCTTGTTGTCATTCATTGACAAGGCTGTGGAGGAAGGCTTCATTAGTCCAAGCGC
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AGTTGCTTCCACTTGTGTGTGTGCTTTCCAG**G**AGTACCTCCCCTGCCATGAAACAGCTGCCCC
CAAGCTAAACTGGGAGATTGAACAGCTAAGTTGCCCTCCACAATGTGATATATCGACA**TGA**

>c28 **PoLOG_2 - Biblioteca LIB15042**

ATGGAAGAGATCAAGTCCCGGTTTAAGAGGATTTGTGTGTTTTGTGGTAGCAGTTCCGGCAA
GAAAGCTACTTATCAAGAAGCTGCAGTTGAGCTGGGGAAGGAAAT**G**GTAGATATACCATCTGAA
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TTGAATCAATCCTCCGGGAGCCAATACCATTATATCTTCACCCTTTTTTCTTGACTTTTTTCTCTGTTTTAGA
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CTCATGTTCATTC**TAG**

>c8 **PoLOG_3 - Biblioteca LIB15042**

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>c1345 **PoLOG_4 - Biblioteca LIB15042**

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>c673 **PoLOG_5a - Biblioteca LIB15042**

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>c7135 **PoLOG_5b - Biblioteca LIB15042**

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>c183 **PoLOG_7 - Biblioteca LIB15042**

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>c545 **PoLOG_8 - Biblioteca LIB15042**

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>c1545 **PoLOG_10 - Biblioteca LIB15042**
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>c1907 **PoLOG_11 - Biblioteca LIB15042**
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>c2375 **PoCKX_1a - Biblioteca LIB15042**
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>c74 **PoCKX_7a - Biblioteca LIB15042**

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>c100 **PoCKX_7b - Biblioteca LIB15042**

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>c227 **PoRR3 - Biblioteca LIB15042**

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>c1761 **PoRR4 - Biblioteca LIB15042**

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>c36 **PoRR5 - Biblioteca LIB15042**

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>c1441 **PoRR6 - Biblioteca LIB15042**

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>c72 **PoRR8 - Biblioteca LIB15042**

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>c2947 **PoRR9 - Biblioteca LIB15042**

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>c971 **PoRR16a - Biblioteca LIB15042**

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>c1037_78 **PoRR11a - Biblioteca LIB15042**

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>c739 **PoRR18a - Biblioteca LIB15042**

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>c7945 **PoRR18b - Biblioteca LIB15042**

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>c1287 **PoRR21 - Biblioteca LIB15042**
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Sequências genômicas dos genes relacionados ao metabolismo e resposta a giberelinas em formato fasta:

>c213 **PoGA2ox2 - Biblioteca LIB15042**

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>c307 **PoGA2ox3 - Biblioteca LIB15042**

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>c397 **PoGA2ox4a - Biblioteca LIB15042**

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>c2737 **PoGA2ox4b - Biblioteca LIB15042**

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>c1937 **PoGA2ox6a - Biblioteca LIB15042**

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>c2547 **PoGA2ox6b - Biblioteca LIB15042**

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>c4764 **PoGA2ox7 - Biblioteca LIB15042**

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>c271 **PoGA2ox8 - Biblioteca LIB15042**

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>c2081 **PoGA3ox1 - Biblioteca LIB15042**
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>c2205 **PoGA3ox2 - Biblioteca LIB15042**
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>c585 **PoGA3ox3 - Biblioteca LIB15042**

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>c102 **PoGA3ox5 - Biblioteca LIB15042**

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CTAGTGTGCTTCACCGCGTGGTAATGAAAGAGACCAAACAAAGGTTGTCCGTGGCATATTTCT
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AGATTAGAATC**TAG**

>c239 **PoGA20ox1 - Biblioteca LIB15042**

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>c6521 **PoGA20ox2 - Biblioteca LIB15042**

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>c555 **PoGA20ox3 - Biblioteca LIB15042**
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>c137 **PoGA20ox4 - Biblioteca LIB15042**
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>c321 **PoGA20ox5 - Biblioteca LIB15042**

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>c3304 **PoGID1a - Biblioteca LIB15042**

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>c110 **PoGID1b1 - Biblioteca LIB15042**

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>c1489 **PoGID1b2 - Biblioteca LIB15042**

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>c41 **PoDELLA1 - Biblioteca LIB15043**

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AGAGACACGAGACGCTGTCCCAGTGGAGGACCCGGTTCGATTCCGCTGGGTTTGTCCCTGTT
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>c957 **PoDELLA2 - Biblioteca LIB15042**

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>c1041 **PoDELLA3 - Biblioteca LIB15042**

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>c1997 **PoDELLA5 - Biblioteca LIB15042**
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APÊNDICE D – SEQUÊNCIAS PROTEICAS

Sequências proteicas dos genes relacionados ao metabolismo e resposta a citocinina em formato fasta

> c2900 PoIPT_2
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> c677 PoIPT_3A
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> c1471 PoIPT_6
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>c673 PoLOG_5a
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Sequências proteicas dos genes relacionados ao metabolismo e resposta a giberelina em formato fasta

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APÊNDICE E – CURVAS DE MELTING

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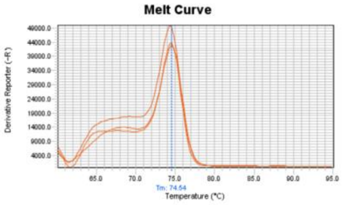

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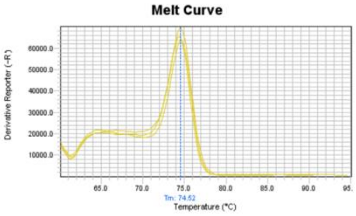

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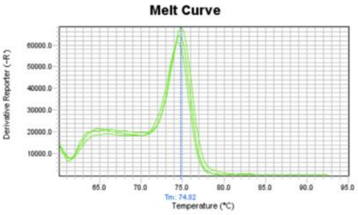

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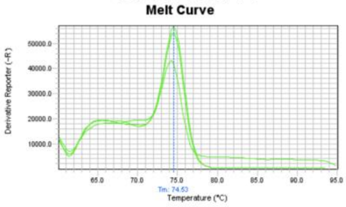

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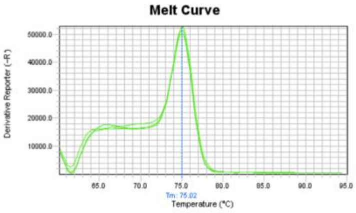

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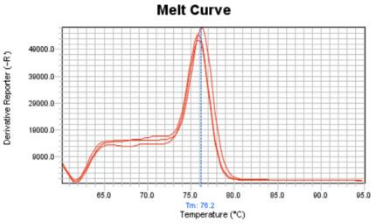

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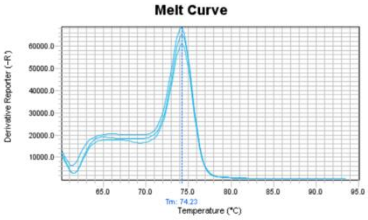

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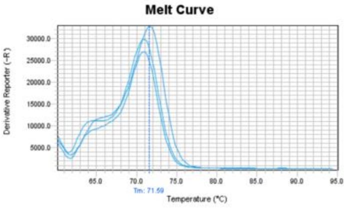

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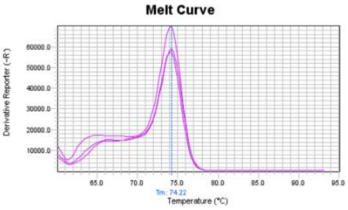

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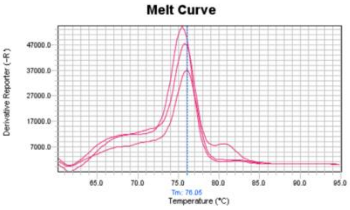

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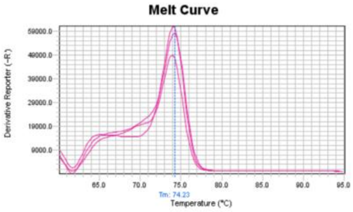

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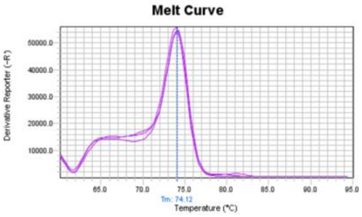

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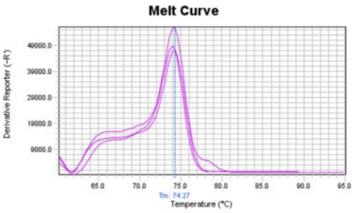

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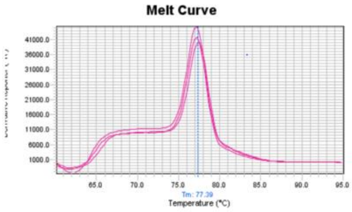

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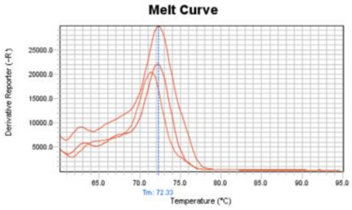

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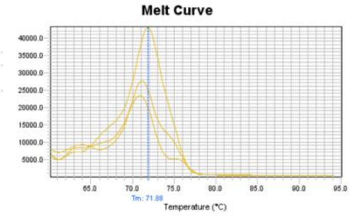

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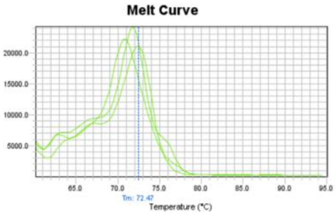

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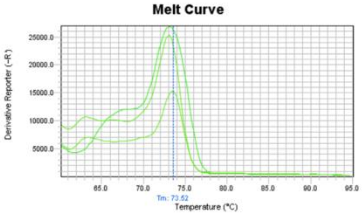

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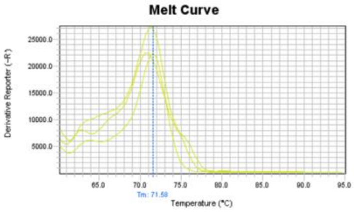

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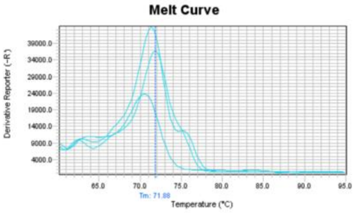

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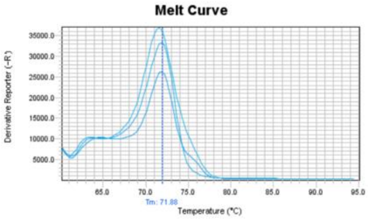

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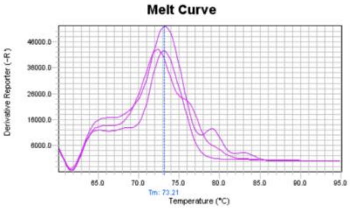

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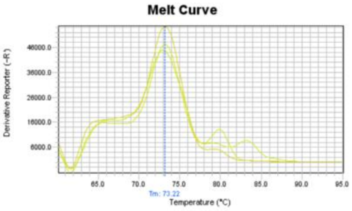

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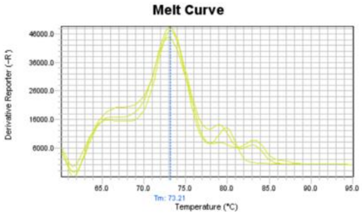

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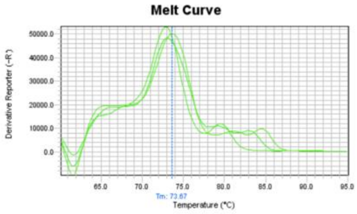

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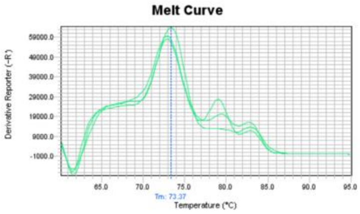

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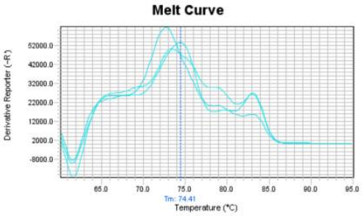

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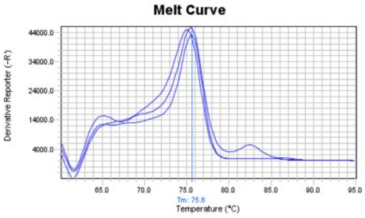

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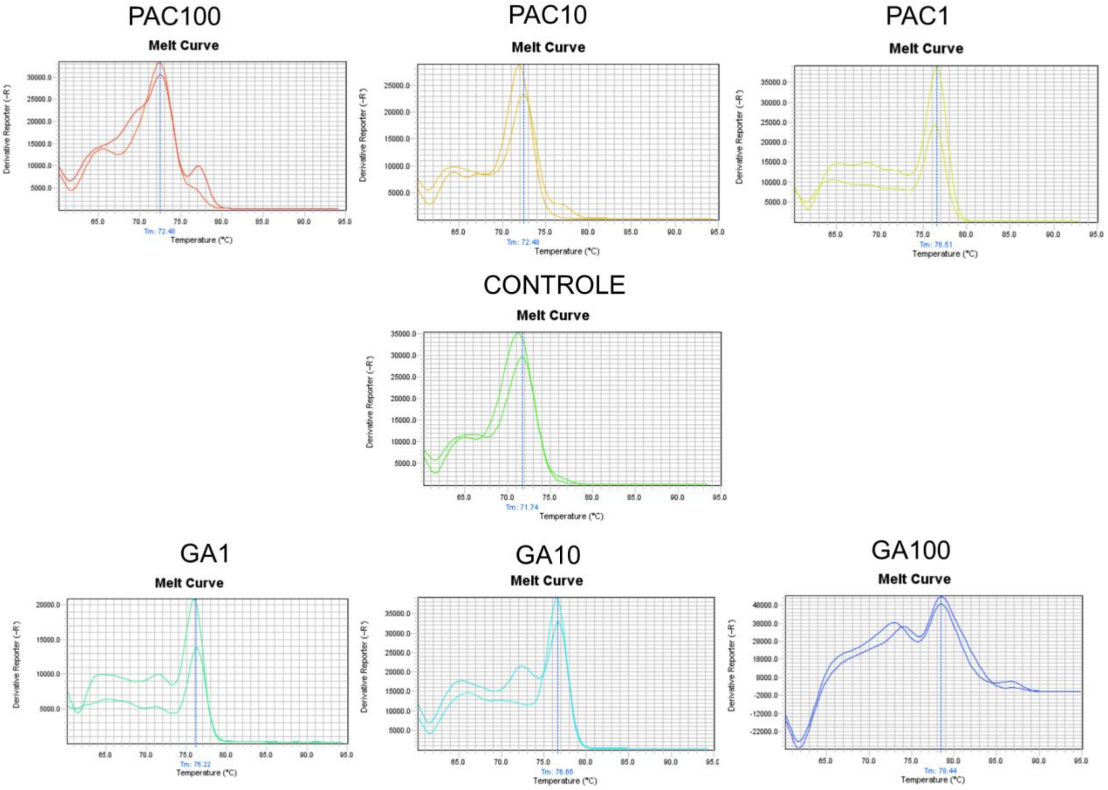

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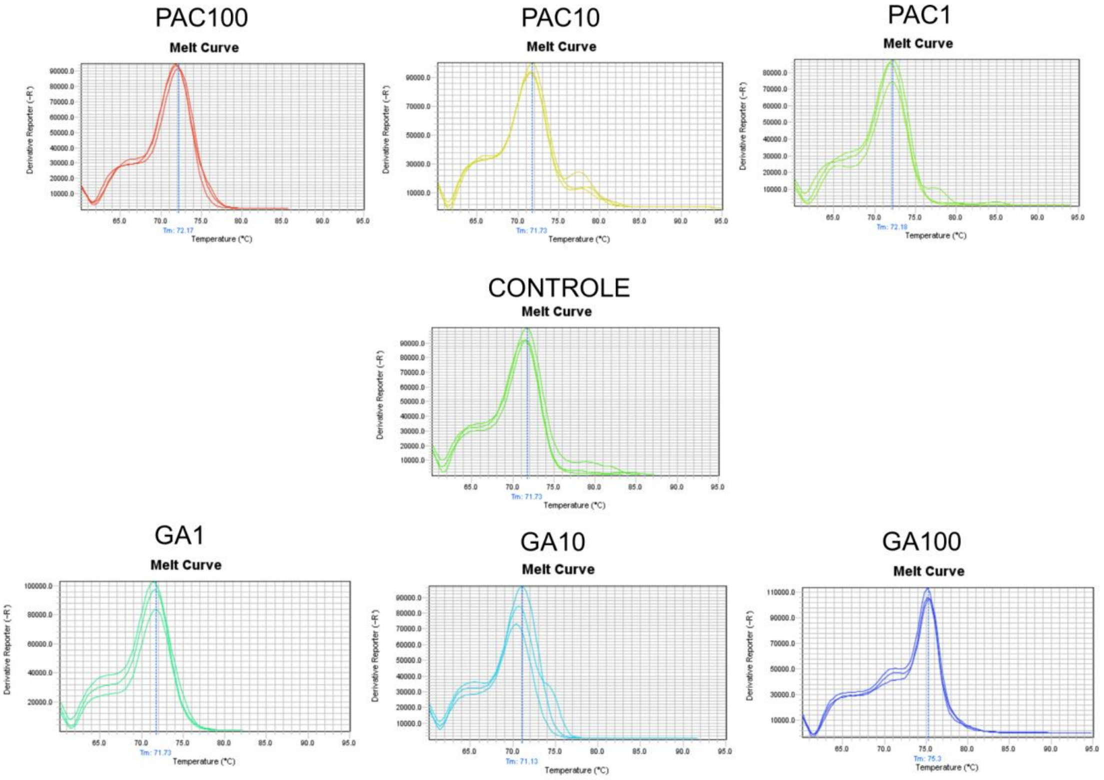

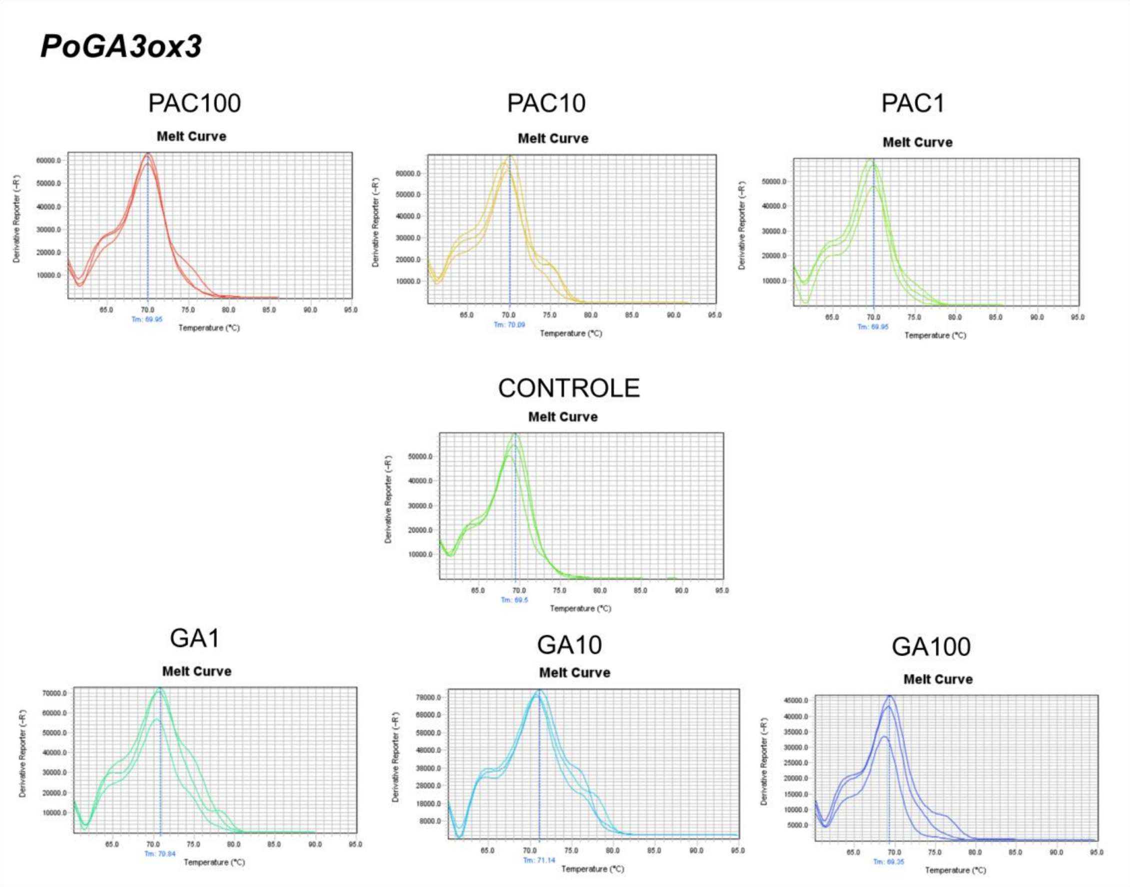
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CONTROLE
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Temperature (°C)

ANEXOS

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