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Jacalin lectin *At5g28520* is regulated by ABA and miR846

Fan Jia and Christopher D. Rock*

Department of Biological Sciences; Texas Tech University; Lubbock, TX USA

Keywords: alternative splicing, microRNA, root, abscisic acid, plant development, pri-miRNA

Abbreviations: ABA, abscisic acid; AGO, Argonaute; bZIP, basic leucine zipper transcription factor; DCL, Dicer-Like; GUS, *Escherichia coli* β-glucuronidase gene *uidA;* PP2C, protein phosphatase type 2C; pri-miRNA, primary *MIRNA* transcript; Pro-, promoter; RACE, Rapid Amplification of cDNA Ends; RNAi, RNA interference; SGS3, Suppressor of Gene Silencing3; TSS, transcription start site

Plant microRNAs (miRNAs) are important regulators of development and stress responses and are oftentimes under transcriptional regulation by stresses and plant hormones. We recently showed that polycistronic *MIR842* and *MIR846* are expressed from the same primary transcript which is subject to alternative splicing. ABA treatment affects the alternative splicing of the primary cistronic transcript which results in differential expression of the two miRNAs that are predicted to target the same family of jacalin lectin genes. One variant of miR846 in roots can direct the cleavage of *AT5G28520,* which is also highly upregulated by ABA in roots. In this addendum, we present additional results further supporting the regulation of *AT5G28520* by *MIR846* using a T-DNA insertion line mapping upstream of *MIR842* and *MIR846*. We also show that *AT5G28520* is transcriptionally induced by ABA and this induction is subject to ABA signaling effectors in seedlings. Based on previous results and data presented in this paper, we propose an interaction loop between *MIR846*, *AT5G28520* and ABA in roots.

microRNAs (miRNAs) are ~21 nucleotide (nt)-long, single-stranded small RNAs that play important regulatory roles in eukaryotes. miRNAs bind to complementary target mRNAs to promote their cleavage post-transcriptionally or to interfere with translation.[1] Plant miRNAs are important regulators of development and stress responses and are oftentimes regulated by stresses and plant hormones such as auxin and abscisic acid (ABA).[2-4] It is remarkable that miRNA and RNAi effectors *AGO1, AGO2* and *DCL1* are targeted by miR168, miR403 and miR162, respectively,[5-7] whereas *DCL2* and *SGS3* (in legumes and soybean, respectively) are targeted by miR1507/1515 and miR2118,[8-10] and *DCL1* encodes miR838 in its intron,[11] underscoring the evolutionary importance of recruitment of RNAi into homeostatic feedback circuits. Recently we and others have shown that besides transcriptional regulation, some *MIRNA* genes (e.g., *MIR400, MIR842* and *MIR846*) are also regulated post-transcriptionally by alternative splicing.[12,13] These miRNAs are found only in *Arabidopsis* and closely related species,[14,15] raising broad questions about *MIRNA* evolution and its functional significance for the targets and their regulation by RNAi crosstalk networks.[16] Recent work on tomato[17] shows unexpected positive correlations between miRNAs and their predicted targets, supporting the notion that there are other processes (e.g., feedback loops) that can impact miRNAs as canonical negative regulators.

We found that polycistronic *MIR842* and *MIR846* are transcribed from the same primary transcript that produces three different splicing isoforms. ABA affects the alternative splicing of the pri-miRNA and thereby represses the expression of the miRNAs.[13] We also showed that *AT5G28520,* a gene encoding a predicted target jacalin lectin[10,18] is cleaved, possibly by a variant "isoMIR" of miR846 in roots. RNA gel blots showed several-fold upregulation of *AT5G28520* by ABA, but real-time PCR experiments demonstrate *AT5G28520* is highly (~50-fold) upregulated within a few hours (**Fig. 1A**). Real-time PCR also showed that ABA treatment repressed pre-miR846 with the strongest (60% reduction) effect observed after three hr exposure to 10 μM ABA (**Fig. 1B**). Furthermore, in the absence of exogenous ABA, pre-miR846 levels decreased after 24 h (**Fig. 1B**) when the expression of *AT5G28520* was elevated (**Fig. 1A**), which is consistent with a causal relationship. However, a 50-fold upregulation of *AT5G28520* by ABA within hours raises questions about whether this induction is by miRNA action alone or if some other type of regulation, for example a positive feedback on transcription initiation,[19] might be involved.

To further study the function of miR842 and miR846, we searched on TAIR (www.arabidopsis.org) and identified a T-DNA insertion line[20] CS815868 which carries an insertion upstream of *MIR842* and *MIR846*, suggesting it may

*Correspondence to: Christopher D. Rock; Email: chris.rock@ttu.edu
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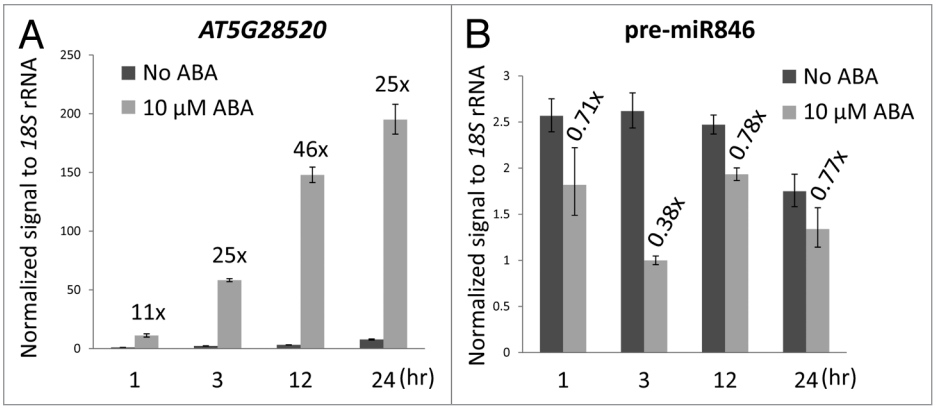

Figure 1. Real-time PCR results showing the ABA-regulated expression of (**A**) *AT5G28520* and (**B**) pre-miR846 in 10-d-old seedlings over 24 h. Numbers above the bars indicate fold changes (comparing to no ABA at the same time point). Error bars are ± s.d., n = 3.

function as an activation-tagged allele. Analysis of the flanking sequence and a genomic Southern blot showed that this T-DNA is inserted near the transcription start site (TSS) of *MIR842* and *MIR846* (**Fig. 2A and B**). 5' RACE showed that the TSS is altered (a 40 nt rDNA-like insertion fragment; data not shown) but pre-miR842 is otherwise intact in CS815868 (**Fig. 2A**). Real-time PCR showed enhanced expression of pre-miR842 and pre-miR846 in roots of CS815868 (**Fig. 2C**) while *AT5G28520* mRNA was reduced (**Fig. 2D**), supporting a causal effect of elevated miR842 and/or miR846 expression on downregulation of *AT5G28520*. This supports our claim[13] that miR846 can direct the cleavage of *AT5G28520*, which is subsequently degraded.

To study the transcriptional regulation of *AT5G28520*, transgenic plants were engineered[21] that express the reporter gene GUS under control of the *AT5G28520* promoter. GUS staining of 10-d-old Pro-*AT5G28520:GUS* seedlings had no detectable GUS activity in the absence of exogenous ABA (**Fig. 3A**). When treated with ABA (30 µM, 4 hr), strong GUS activity was observed in roots, especially in lateral root primordia, but not in leaves (**Fig. 3B and C**). RNA gel blot analysis further showed that this induction was strongly suppressed by ABA-insensitive signal transduction mutants such as PP2Cs *abi1-1* (75% reduction), *abi2-1*[22] (84% reduction), APETALA2 domain *abi4-1*[23] (35% reduction) and bZIP *abi5-1*[24] (32% reduction), whereas B3 domain *abi3-1*[25] mutant had a relatively weak effect (12% reduction) (**Fig. 2D**), consistent with previous results showing

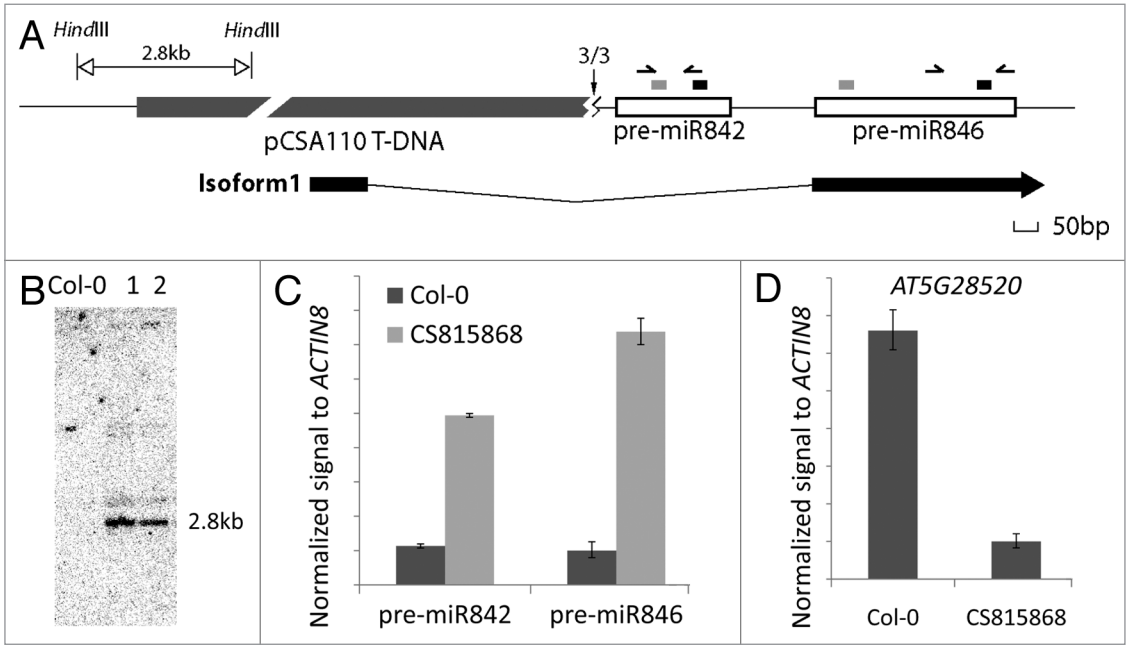

Figure 2. *AT5G28520* is downregulated in CS815868 T-DNA insertion plants, which overexpress pre-miR842 and pre-miR846. (**A**) Genomic structure around *MIR842* and *MIR846* in T-DNA insertion line CS815868. TSS revealed by 5' RACE is shown with a vertical black arrow (numbers are sequenced clones mapping to site out of the total clones sequenced). The zigzag below the arrow represents a 40 bp sequence found that does not map to the T-DNA and has homology to rDNA. Open boxes represent pre-miR842 and pre-miR846. The short gray rectangles above the open boxes represent miRNA* and short black rectangles represent mature miRNA sequences. Isoform 1, which is the most abundant splice variant expressed from this locus in wild type is shown below. Black boxes represent exons. Horizontal arrows represent primers used for real-time PCR of pre-miRNAs in (**C**). (**B**) Genomic Southern blot showing single insert in CS815868. Lanes 1 and 2 are *Hind*III-digested genomic DNAs from two individual CS815868 plants. Blot was probed with *BASTA* selectable marker gene fragment from the vector. (**C and D**) Real-time PCR results showing the different expression levels of *AT5G28520* (**C**) and pre-miR842 and -miR846 (**D**) in roots of control Col-0 and CS815868 line. Error bar, ± s.d., n = 2.

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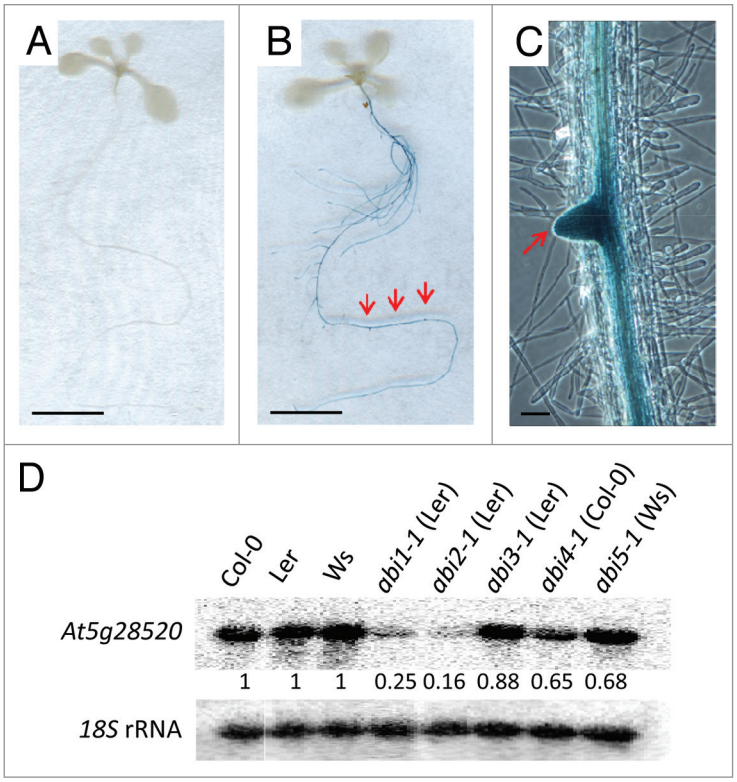

Figure 3. *AT5G28520* is upregulated transcriptionally by ABA. (**A–C**) GUS staining of *Pro-AT5G28520:GUS* transgenic seedlings after 4 h treatment in the absence (**A**) or presence (**B**) of exogenous 30 μM ABA. A lateral root primordium in (**B**) is imaged under higher magnification light microscope in (**C**). Red arrows point to lateral root primordia. Scale bars in (**A and B**) represent 5 mm. Scale bar in (**C**) represents 1 mm. (**D**) Blot of total RNA from root samples from different ABA signaling mutants and their corresponding wild type controls treated with 30 μM ABA for 3 hr. Numbers below the panels are normalized band intensities compared with *18S* rRNA signal.

that *ABI3* is expressed in seeds and *ABI5* expression decreases progressively after germination.[26]

Together with the results presented in our recent paper,[13] we have shown that: (1) miR846 and *AT5G28520* are co-expressed in roots; (2) a possible isomer variant (5' shifted) of miR846 directs the cleavage of *AT5G28520* in the absence of ABA; (3) *AT5G28520* is downregulated in an *MIR842* and *MIR846* T-DNA activation-tagged overexpression allele; (4) ABA upregulates *AT5G28520* transcriptionally and this regulation requires the functions of ABI1, -2, -4 and -5; and (5) ABA downregulates miR846 post-transcriptionally by alternative splicing. Based on these results, we propose a model in which ABA, *MIR846* and *AT5G28520* form a regulatory network in roots (**Fig. 4**). In the absence of exogenous ABA (and presumably low concentrations of endogenous ABA), expression of *AT5G28520* is low and the expression of miR846 would direct the jacalin mRNA to be endonucleolytically cleaved or possibly subject to translational repression. In the presence of exogenous ABA (or high endogenous ABA concentrations, e.g., in response to stress), transcription of *AT5G28520* is elevated, and at the same time miR846 biogenesis is repressed by alternate splicing, which results in *AT5G28520* mRNA accumulation. This synergistic effect could account for the rapid ~50-fold induction of *AT5G28520* by exogenous ABA at as low as 1 μM, which is within the physiological range found in plants.[27] We speculate that biogenesis of pre-miR842/846 by complexes containing effectors of ABA sensitivity and splicing such as ABA hypersensitive1/cap-binding protein80,[28] hyponastic leaves,[29] serrate,[30] argonaute[31] and others may be important for miR846 function. In addition, ABA may also repress the expression of the *MIR842-MIR846* cistron transcriptionally. The function of jacalin lectins is poorly understood and recent studies link their activities to virus resistance and biotic stress.[32,33] Further work is needed to understand the function of *AT5G28520* and the importance of RNAi regulatory networks to ABA signaling in root development and environmental stress responses.

Materials and Methods

Plasmid construction. For the promoter analysis of *AT5G28520*, a 1.5 kb sequence upstream of the start codon was PCR-amplified using PrimeSTAR HS DNA polymerase (Takara) and inserted between the *Hind* III and *Bam*HI sites in pBI121, replacing the *35S* promoter which drives *uidA* GUS reporter gene expression. Oligonucleotide primers were designed using "Perlprimer" (perlprimer.sourceforge.net) and synthesized commercially (Sigma). A list of primers used in the study is provided in **Table 1**.

Plant material and growth conditions. The accessions used in this study are listed as follows: Col-0 [CS60,000], Ler-0 [CS20], Ws-2 [CS2360], *abi1-1* [CS22], *abi2-1* [CS23], *abi3-1* [CS24], *abi4-1* [CS8104], *abi5-1* [CS8105], CS815868 and were obtained from the Arabidopsis Biological Resource Center (abrc.osu.edu). *Arabidopsis thaliana* seeds were soaked in water and kept in the dark at 4°C for 3 d before transferring to soil. The growth condition was 21°C with a 16 h light and 8 h dark cycle. For promoter analysis, plants were transformed with *Pro-AT5G28520:GUS* constructs first electroporated into *Agrobacterium tumefaciens* strain GV3101 and then transferred to the plants using the floral dip method.[21]

For ABA treatments, seeds were sown on plates containing 0.5× Murashige and Skoog salts (Research Products International) 1% sucrose and 0.5% phytagel (Sigma). Plates were kept in the dark at 4°C for 3 d before transferring into a growth chamber. The growth condition was 21°C with continuous light. Plates were kept in the chamber for 10 d before spraying with ABA solutions. ABA [(±)-Abscisic acid, 98%; ACROS Organics] solutions were diluted with water from a 100 μM stock in 70% ethanol. The same amount of 70% ethanol was added to water to spray the control group.

β-Glucuronidase GUS assays. Plant samples were developed at 37°C for 12 h with a 1 mM solution of the indigogenic GUS substrate 5-bromo-4-chloro-3-indolyl b-D-glucu-ronide (X-Gluc; Rose Scientific) in 50 mM KH_2PO_4 (pH 7.0), 0.1 mM EDTA, 0.5 mM ferricyanide, 0.5 mM ferrocyanide, 0.05% sodium azide, 0.1% Triton X-100. After staining overnight,

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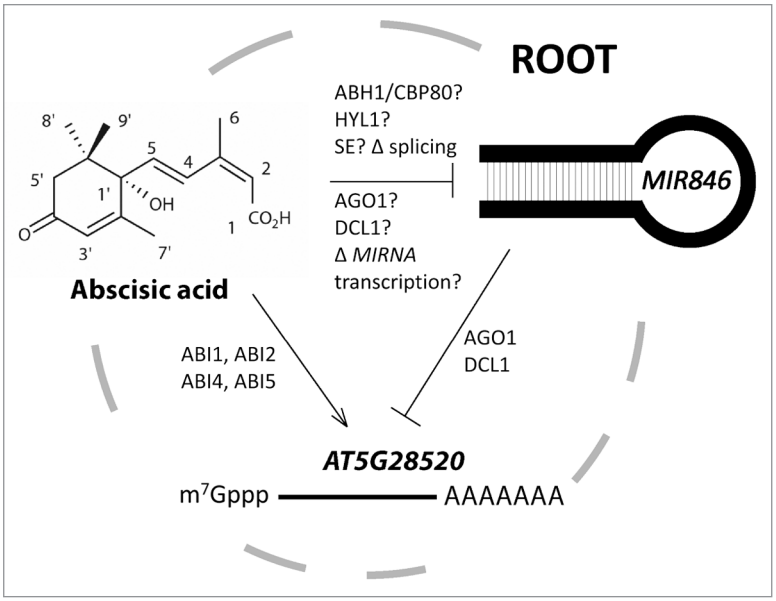

Figure 4. A model showing the possible interactions between RNAi pathways and *MIR846*, *AT5G28520* and ABA in roots. A variant of miR846 is normally expressed that directs the post-transcriptional cleavage/repression of *AT5G28520* in the absence of ABA; ABA induces the expression of *AT5G28520* transcriptionally and simultaneously represses miR846 by directing alternative pri-miR846 splicing (Δ = change) and possibly modulating biogenesis through RNAi effectors known to impact ABA sensitivity by unknown mechanisms. AGO1 and DCL1 are known to act downstream of pre-miR846 hairpin biogenesis. Transcriptional repression (Δ) of *MIR846* by ABA may also be involved.

samples were immersed in 70% ethanol overnight. Samples were then mounted in 30% glycerol on microscope slides for imaging with a dissecting microscope or with an Olympus BX41 light microscope for high magnification and documented using QCapture software (v2.68.6, Silicon Graphics).

Real-time PCR. Total RNA from roots of 10-d-old seedlings was extracted with Iso-RNA Lysis Reagent (5 PRIME). Four μg total RNA was digested with RQ1 RNase-free DNase (Promega) and reverse transcribed by MMLV reverse transcriptase (Promega) with random primers (Promega). Real-time PCR was performed using FastStart Universal SYBR Green Master (Rox) (Roche) according to the supplier's protocol. PCR reactions were run on an ABI7000 (Applied Biosystems) instrument with default settings and results were analyzed with affiliated software. cDNA preparation was the same as for reverse transcriptase-PCR except that random primers (Promega) was used in reverse transcription.

5' RACE. RACE experiments were performed with GeneRacer Kit (Invitrogen) according to the manufacturer's specification.

Southern hybridization. Genomic DNA was isolated from Col-0 plants and two individual CS815868 plants using CTAB (Hexadecyl trimethyl-ammonium bromide, ACROS Organics). 15 μg genomic DNA was used for each *Hind*III digestion. The samples were resolved on a 0.7% agarose gel and blotted to a Hybond-N$^+$ membrane (GE Healthcare) according to the supplier's protocol. *BASTA* template was amplified using primers "BASTA_F" and "BASTA_R" from CS815868 genomic DNA and was eluted after excision of the band from an agarose gel. Probes were synthesized using Random Primer DNA Labeling Kit (Takara) with [α-^{32}P]-dCTP (PerkinElmer). Hybridization was performed with the PerfectHyb Plus hybridization buffer (Sigma) according to the manufacturer's instructions. A storage phosphor screen (GE Healthcare) was used for autoradiography and it was scanned using a Storm 860 PhosphorImager (GE Healthcare).

Northern hybridization. Samples of 10 μg total RNA were resolved on a 1.2% denaturing agarose gel and blotted to a Hybond-N$^+$ membrane (GE Healthcare) according to the supplier's protocol. *At5g28520* template was amplified using primers "AT5G28520CDS_F" and "At5g28520CDS_R" from a cDNA library and was eluted after excision of the band from an agarose gel. Probes were synthesized and blots processed as described for genomic DNA gel blots.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

Acknowledgments

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Table 1. Primers used in this study

promoter cloning, At5g28520	Pro5g28520_F	ACC AAG CTT AGA GCT TCA AAT CAT T
	Pro5g28520_R	AAC GGA TCC CAC GAA CTG TTT TGA
Real-time PCR	Pre846_F	ACG ATT GGA AGC TGA ATG GTT GCG
	Pre846_R	CGA ATT TAC CGG GAT ACA CGA GCA
	Pre842_F	TAA GCG GGA TGA TGA ATC CGA CCA
	Pre842_R	TGA TGG TGT TTC GAT CCC TGG ACA
	At5g28520_QRT_F	GTC GTG AAG GCA TTC AGT ACG TCA
	At5g28520_QRT_R	TTG TGT GAA TCC TCC TCT ACC CGA
	18S_F	AAA TAC CGC GGC TGC TGG CA
	18S_R	CGG CTA CCA CAT CCA AGG AA
	ACTIN8_F	GGA ATG GTT AAG GCT GGA TTC G
	ACTIN8_R	ACG CAT CTT TCT GAT TCA TCC C
5' RACE	5RACE1	CGA ATT TAC CGG GAT ACA CGA GCA
	5RACE2	CCT TGA ATG AAA CCG GAT GTG GCA
	5RACE3	CGA GGC GGT TAA TCT CAA ACT GCT
	5RACE4	TGA TGG TGT TTC GAT CCC TGG ACA
Northern	At5g28520CDS_F	ATG GCT CAG AAG TTA GAA GCA ATA G
	At5g28520CDS_R	TCA CTC GCG CGT GAT GGG C
	18S primer pair	same as 18S_F and 18S_R pair used in real-time PCR
Southern	BASTA_F	GGT CTG CAC CAT CGT CAA CC
	BASTA_R	CCA GAA ACC CAC GTC ATG CC

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