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Unique transcriptome features of pea (*Pisum sativum* L.) lines with differing responses to beneficial soil microorganisms

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BACKGROUND: Garden pea (*Pisum sativum* L.) possesses the ability to form beneficial symbioses with various soil microorganisms. However, different pea cultivars, genotypes, and lines gain more or less benefit from these interactions, so the trait named "efficiency of interaction with soil microorganisms" (EIBSM) was suggested to describe this phenomenon. The molecular mechanisms underlying the manifestation of the EIBSM trait are not properly studied, and only few works focusing on plant responses to combined microbial preparations have been published to date.

METHODS: Eight pea lines previously described as contrasting in manifestation of the EIBSM trait were grown in pots with soil under combined inoculation with nodule bacteria and arbuscular mycorrhizal fungi, and the transcriptome profiles of the whole root systems of the plants were investigated using 3'MACE RNA sequencing.

RESULTS: The relatedness of the lines inferred from the analysis of transcripts' SNVs (Single Nucleotide Variants) corresponded to the manifestation of the EIBSM trait: three high-EIBSM lines and three low-EIBSM lines formed two distinct clusters. Thus, the gene expression profiles were compared between these two clusters, which enabled identification of transcriptome signatures characteristic for each group. The lines previously described as high-EIBSM have lower symbiotic activity, and the expression levels of pathogen response genes were elevated compared to the lines with low EIBSM.

CONCLUSION: This result suggests that the mechanism of high interaction efficiency may be connected to stricter host control of symbionts, allowing such plants to expend less on the symbioses.

Keywords: transcriptomics; *Pisum sativum* L.; nodule bacteria; arbuscular mycorrhiza; effectiveness of symbiosis.

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Уникальные характеристики транскриптомов линий гороха (*Pisum sativum* L.), контрастных по эффективности взаимодействий с почвенными микроорганизмами

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Горох посевной (*Pisum sativum* L.) способен образовывать симбиозы с почвенными организмами. Для различных сортов, генотипов и линий гороха польза от таких взаимодействия может значительно отличаться, поэтому был предложен термин «эффективность взаимодействия с полезными почвенными микроорганизмами» (ЭВППМ). Молекулярные основы данного признака исследованы недостаточно, и лишь малое число работ было посвящено ответу растения на комбинированные микробные препараты. В работе были использованы восемь линий гороха посевного, отличающихся по признаку ЭВППМ, которые выращивались в сосудах с почвой при инокуляции клубеньковыми бактериями и арбускулярно-микоризными грибами. Транскриптомные профили их корневых систем были исследованы с использованием метода 3'MACE РНК-секвенирования. Степень родства изучаемых линий была определена путем анализа однонуклеотидных вариантов (SNV – Single Nucleotide Variants), три линии с высоким и три с низким показателем ЭВППМ сформировали два хорошо различимых кластера. Экспрессия генов сравнивалась между этими двумя кластерами, что позволило идентифицировать маркерные транскрипты в обеих группах. В группе с высокой ЭВППМ была значительно снижена экспрессия генов, отвечающих за активность симбиоза, а экспрессия генов, связанных с ответом на патогены, была повышена, по сравнению с группой с низкой ЭВППМ. Этот результат указывает на то, что высокая ЭВППМ может быть связана с более жестким контролем симбионтов со стороны растения-хозяина, что позволяет растению тратить меньше ресурсов на поддержание микросимбионтов.

Ключевые слова: транскриптомика, *Pisum sativum* L., клубеньковые бактерии, арбускулярная микориза, эффективность симбиоза.

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ЭКО•ВЕКТОР

BACKGROUND

Pea (*Pisum sativum* L.), like other legumes, forms beneficial symbioses with a wide range of soil microorganisms, including nodule bacteria (rhizobia) and arbuscular-mycorrhizal (AM) fungi [1]. A plant hosts microsymbionts in its tissues and feeds them with photosynthates; rhizobia supply the plant with fixed atmospheric nitrogen, and AM fungi provide water and hardly soluble phosphates [2]. Thus, the genomes of microsymbionts complement the genome of a plant, providing new functions to a newly formed symbiotic system [3].

Pea was domesticated over 10 000 years ago [4]. During pea domestication and subsequent selection and breeding, a large number of pea landraces and, later on, varieties and cultivars with highly differing phenotypes came to be (now, the number of pea accessions in seed collections exceeds 70,000) [5]. Some specific traits, namely, pod dehiscence and seed dormancy, were lost in domesticated peas [6], when seed number, weight, and taste, along with drought-, insect- and disease tolerance, were improved during domestication and further breeding [7]. However, other qualities, such as symbiotic performance, i.e., the ability to effectively interact with beneficial microorganisms, were not actively selected for, thus, the alleles that confer high symbiotic effectiveness may be lacking in a large proportion of the cultured pea accessions available to researchers and agriculture [6].

The response of pea to inoculation with soil microorganisms has been investigated in various lines and cultivars, under mono-inoculation with either rhizobia or AM fungi, or under complex inoculation with both symbionts [8]. The effect of inoculation in terms of increase in plant and seed biomass was often variable and was dependent on experimental conditions and plant genotype, i.e. some genotypes were shown to be more or less responsive to inoculation. Based on the results of pot and field trials, the trait called EIBSM (for Effectiveness of Interaction with Beneficial Soil Microorganisms), defined as the degree of increase in seed biomass under combined inoculation compared to uninoculated control, was suggested as a prospective trait for pea breeding [9].

In last five years, 'omic' technologies, such as proteomics and metabolomics, have been successfully applied to investigate the molecular bases of pea response to microsymbionts and pathogens [10–13]. It was shown that inoculation with rhizobia and/or AM fungi not only improves plant nutrition and seed filling but also can increase the plant's resistance to the pathogenic fungus *Didymella pinodes* [10]. Additionally, two different strategies of response to complex inoculation with rhizobia and AM fungi were described for different pea genotypes: under inoculation, the 'responsive' genotype prolonged the seed filling stage, which led to increase in seed biomass, while the 'nonresponsive' genotype, as opposite, shortened the seed maturation period [12]. However, the above-mentioned studies were performed either on a single pea cultivar or on a pair of cultivars, which does not allow general conclusions about the molecular base of the responses to microsymbionts. In the present work, using a modified RNAseq, 3'MACE-seq [14], we analysed the transcriptomes of the whole root systems of eight genotypes previously characterized with respect to EIBSM trait, and described the transcriptome profiles and SNVs (single nucleotide variants) characteristic for 'high-EIBSM' genotypes in contrast to 'low-EIBSM' ones.

MATERIALS AND METHODS

Plant material

The pea lines used for the experiment were chosen based on their EIBSM manifestation, according to [8] (the low- or high-EIBSM labels were designated based on the results of three-year field trials, 2002–2004, Orel region, Russia). The line k-3064 was obtained from the collection of cultivated peas of the N.I. Vavilov All-Russian Institute of Plant Genetic Resources (VIR), Saint Petersburg, Russia. All other lines originated from the center for Grain Legume Genetics Physiology Research: Pullman, Department of Agriculture, Washington University, USA. The lines were propagated in All-Russia Research Institute for Agricultural Microbiology (Saint Petersburg, Russia). The lines and their phenotype are listed in Table 1.

AM inoculum preparation

The AM inoculum consisted of three *R. irregularis* strains BEG144, BEG53 (both provided by the International Bank for the Glomeromycota, Dijon, France), and ST3 (All-Russia Research Institute for Agricultural Microbiology, Saint Petersburg) [15]. All isolates were cultured individually in a sand/soil mixture (1:1 v/v) using *Plectranthus australis* R. Br. as a host plant. To obtain the inoculum of AM fungi, the seeds of sorghum (*Sorghum* sp.) were surface sterilized with a 0.15% (w/v) aqueous solution of potassium permanganate for 15 min, and transferred to pots, filled with a soil-based substrate (pH 7) containing dried *P. australis* roots colonized with the three above mentioned *R. irregularis* strains. After about 120 days of

Table 1. The pea lines used in this work

Line	Phenotype
Lifter	low-EIBSM
PS9910134	low-EIBSM
PS9910135	low-EIBSM
PS9910188	low-EIBSM
k-3064	low-EIBSM
PS810240	high-EIBSM
PS610324	high-EIBSM
PS9910029	high-EIBSM

vegetation, the colonized sorghum roots were separated from the substrate, cut into 1 cm pieces, dried and mixed with the substrate to establish the inoculum.

Plant growth conditions

The seeds were surface sterilized with concentrated sulfuric acid, rinsed with sterile water, germinated on 1% agar-agar medium for three days in darkness at 25°C. Seeds were planted in 5 L pots filled with sod-podzolic light loamy soil (five plants per pot), and inoculated with 150 ml of water suspension (10^6 CFU * l-1) of symbiotic bacteria (*Rhizobium leguminosarum* bv. *viciae* RCAM1026) [16] in combination with prepared inoculum (see previous section), as described in [17]. After that, each of the 5 planted seeds were covered with 9 g of the AM fungal inoculum (see previous section). Before planting, the pots were adjusted to the same weight with soil. The plants were grown under noncontrolled light and temperature conditions in the vegetation house of the All-Russia Research Institute for Agricultural Microbiology, Saint Petersburg (June–August 2016). For the RNA isolation and MACE library preparation plants were harvested at 4 weeks after inoculation. For evaluation of the growth parameters the plants were harvested at the mature seed stage (3 months after planting). Data processing and statistical evaluation was performed in the R environment [18]. No significant changes in seed weight or whole plant weight were observed.

RNA extraction, library preparation and sequencing

The root systems of the plants at 4 weeks after inoculation were extracted from soil, the substrate was washed away with running water, and then the roots were snap-frozen in liquid nitrogen. The material was ground using mortar and pestle, the RNA was isolated using the Trizol reagent (Thermo Fisher Scientific, USA) according to the manufacturer's protocol with minor changes. The RNA quality was assessed visually using gel electrophoresis in 1.5% agarose, and the concentration of RNA was measured using a Qubit Fluorometer and Qubit RNA BR Assay Kit (Thermo Fisher Scientific, USA). The MACE library preparation using the MACE kit v 1.0 and library sequencing on an Illumina HiSeq2000 platform were performed by GenXPro GmbH (Frankfurt am Main, Germany).

Bioinformatic analysis

The FastQC (version 0.11.8) and multiqc [19] were used to assess the quality of raw reads. Adapters, low quality reads, human and bacterial contaminants were removed as in [20]. Paired-end reads were mapped to the reference genome of the cv. Caméor [21] and gene expression was measured using STAR (version 2.7.3a.) [22] with the -quantMode GeneCounts option enabled. Differential gene expression analysis was performed using the DESeq2 [23] package in the R environment. Mercator online tool [24] was used to assign functional categories to the differentially expressed genes.

To analyze the SNP distribution in the pea lines, the reads were mapped against the reference using the bwa algorithm. The resulting bam files were used for variant calling using the deepvariant pipeline [25]. All the generated gvcf files were combined using the GLnexus pipeline into a single VCF file [26]. The VCF file manipulations were performed in the R environment with the vcfR and adegenet packages [27, 28].

Data availability

The sequence data have been uploaded to the NCBI database. The BioProject number is PRJNA685796, raw Illumina data has the following SRA accession numbers SRR13260340-SRR13260347.

RESULTS AND DISCUSSION

Analysis of SNV profiles for the lines

Since the 3'MACE-seq enables both precise gene expression level and SNV analysis [14], the genetic relatedness of the lines was estimated first. On the base of all the SNVs found by mapping of reads to the pea genome, a genetic distance tree was built (Fig. 1).

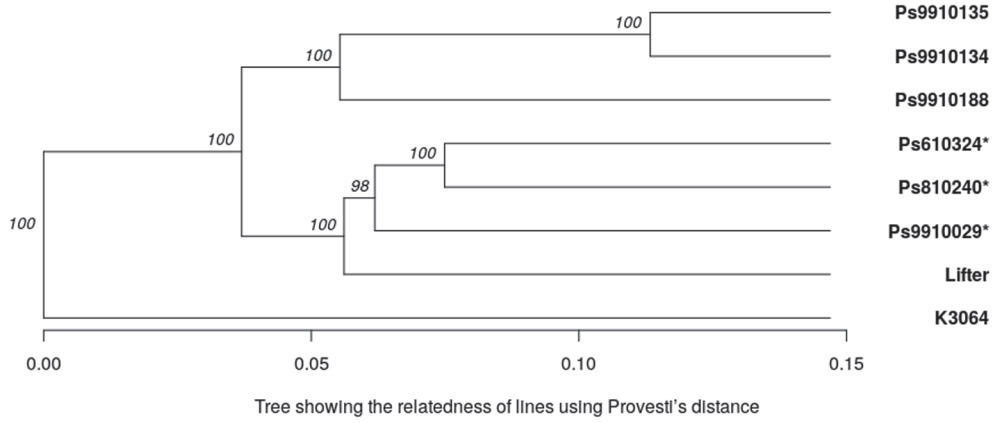

Fig. 1. The tree shows the genetic relatedness of pea lines. The distance was calculated using Provesti's distance algorithm of the *poppr* [28], the bootstrap values are presented in the nodes of the tree. The high-EIBSM lines are denoted with "*"

As can be seen in Figure 1, the 'high-EIBSM' lines formed a well-defined group. Three lines with low EIBSM, 'Ps9910188', 'Ps9910134' and 'Ps9910135', also formed a cluster, whereas two other lines, 'Lifter' and 'k-3064', were not in either of the groups. Since the manifestation of the EIBSM trait might be determined by different mechanisms in nonrelated genotypes, only two groups were analysed further. Hereinafter, the 'high-EIBSM' and the 'low-EIBSM' characteristics refers to the groups of three genotypes.

No nonsense or missense mutations were found during the SNV analysis in either of the 8 lines, which can be in part explained by the fact that the MACE reads are synthesised mainly on the 3' end on the mRNA molecule, so a good portion of them lie outside of the coding sequence, thus making any nucleotide change not influence the coding capability of the transcripts.

Analysis of transcriptome profiles of the lines

STAR algorithm was used to map and quantify the reads, the sequencing and mapping results are presented in Table 2.

The transcriptome analysis was performed using the DegSeq2 package. To verify the expression uniformity and for quality control, PCA was performed for the samples in the two groups. The results for the PCA are presented in the Fig. 2.

The two groups are distinctly visible on this graph, as 58 percent of the variance is explained by the first component. It was decided to perform differential gene expression analysis treating each three lines of a single phenotype as a group for differential gene expression. The expression of genes, associated with symbiotic processes, i.e., mycorrhizal and nodule symbiosis formation, was investigated to determine the symbiotic status of the contrasting lines. Six of these genes (*Vacuolar iron transporter homolog 4, Early nodulin-12B, Nodulin-1, Early nodulin-16, Probable 2-isopropylmalate synthase, Early nodulin-5*), were significantly (Padj < 0,05) downregulated in the high-EIBSM group. That might be the evidence of the less developed nodule symbiosis in the "high-EIBSM" plants.

Table 2. The results of sequencing and read mapping

Line	Number of reads, mln	Aligned, %	Length, bp
Ps9910029	8.7	72.9	66
Ps810240	7.1	67.8	66
Ps610324	8.4	67.7	66
Lifter	7.7	62.9	66
Ps9910188	6.4	62.6	66
Ps9910134	8.3	64.2	66
Ps9910135	16.0	73.0	66
K-3064	14.5	69.8	66

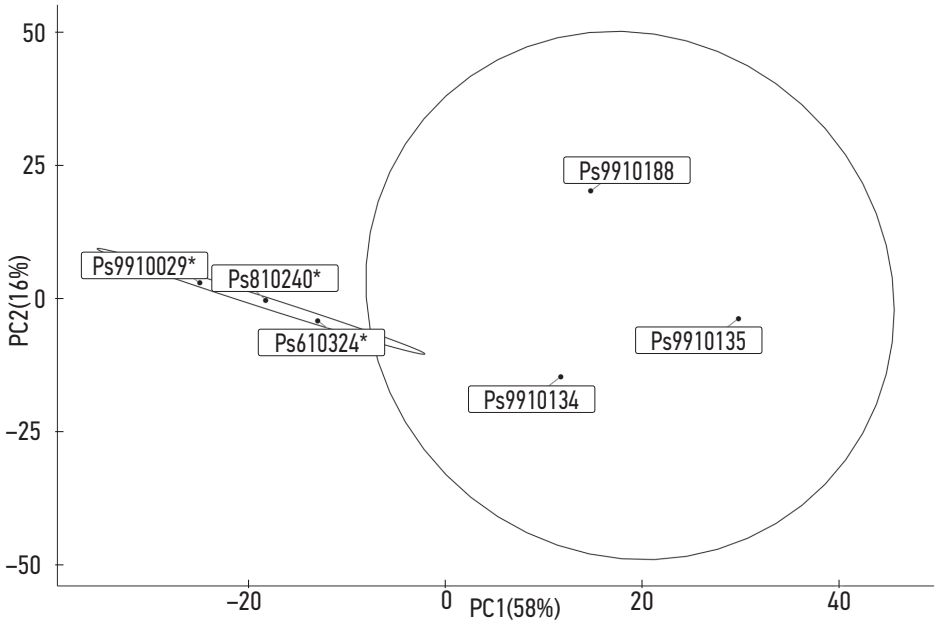

Fig. 2. The PCA plot for the six lines with contrast manifestation of the EIBSM trait. The high-EIBSM lines are denoted with "*", 95% confidence ellipses were built for the two discussed groups

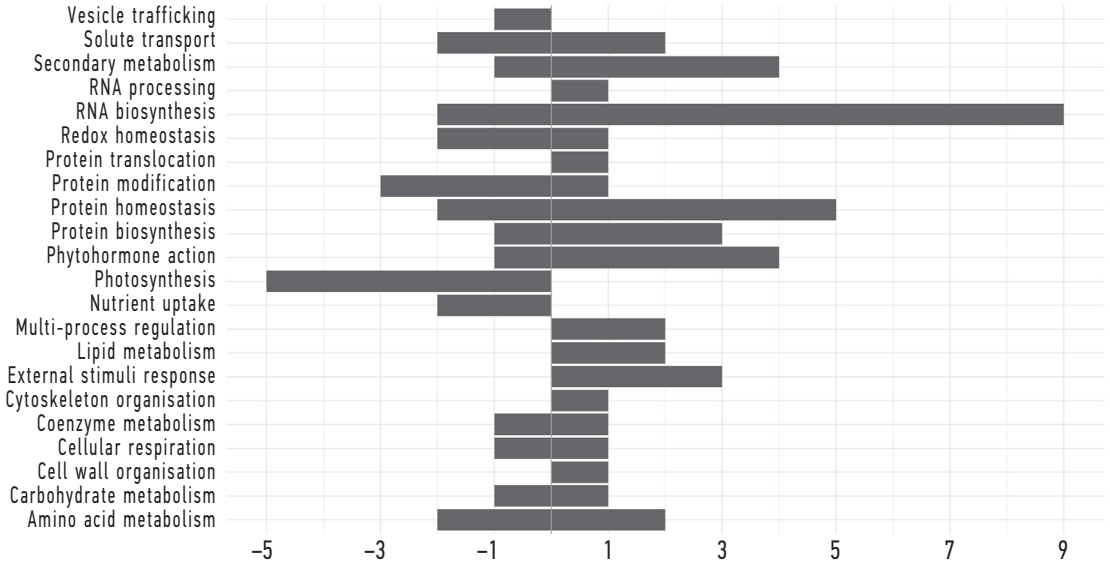

Fig. 3. The functional categories of genes, differing in their expression in EIBSM-contrasting lines. The bars represent the number of genes in the category, the bars to the right are genes with higher expression level in the 'high-EIBSM' lines, and vice versa

A total of 456 genes had significantly (Padj < 0.05) different expression levels between the two investigated groups. Of these, 180 genes were up-regulated, while 276 were down-regulated in the 'high-EIBSM' lines compared to the 'low-EIBSM' ones. For 161 genes, we were able to obtain the Mercator annotation (Fig. 3). As can be seen, in the 'high-EIBSM' lines, the vesicle transport genes, the nutrient uptake genes, and genes annotated as related to photosynthesis, are down-regulated, while multiple phytohormone-associated genes, external stimuli response genes, lipid metabolism genes, and RNA and protein biosynthesis genes are upregulated. These genes, whose expression forms specific 'transcriptome signatures' characteristic for 'high-EIBSM' lines, can be considered important for the effective realization of the symbiotic strategy. The full list of differentially expressed genes can be found at http://cloud.arriam.ru/s/ksQx4dr9ydRsXQo.

The detailed analysis of the differentially expressed genes led us to some preliminary conclusions and speculations on the molecular mechanisms of symbiotic efficiency in the investigated pea lines. As presented in Table 3, 'high-EIBSM' lines show down-regulation of the gene encoding thioredoxin, the ortholog of which is highly active in the nodules of *Medicago truncatula* Gaertn. plants [30]. The next gene strongly down-regulated in 'high-EIBSM' lines is *MSBP1*, which appears to be a potential marker of effective mycorrhizal symbiosis. The orthologous gene in *M. truncatula* (*MtMSBP1*) encodes a membrane-bound steroid-binding protein, probably involved in brassinosteroid signaling [31]. Interestingly, overexpression of the tomato (*Solanum lycopersicum* L.) gene *SlMSBP1* in transgenic tobacco (*Nicotiana tabacum* L.) plants resulted in a decrease in biomass development after mycorrhization of the corresponding transgenic lines [32], which is in agreement with low-responsivity to double inoculation of the pea lines with higher *MSBP1* expression level. Two other down-regulated genes in 'high-EIBSM' lines encode plastid products (components of light harvesting complexes), and their expression level may reflect a reduced activity of plastids in the roots. The same effect, i.e., a decreased expression level in 'high-EIBSM' lines, was recorded for the plastidial glutamine synthetase (*GLN2*) gene [33, 34]. Finally, the down-regulation in 'high-EIBSM' lines was shown for the phytoene synthase (PSY3) gene, which encodes the enzyme catalyzing the rate-limiting step of carotenoid biosynthesis [35]. Carotenoid biosynthesis also occurs in plastids, and in roots, it leads to the production of strigolactones – the signal molecules that promote root colonization by AM fungi [36]. Thus, down-regulation of this

Table 3. Genes differentially expressed between the two EIBSM groups involved in symbiotic processes. The *M. truncatula* gene IDs are presented according to [37]

Gene	Orthologous gene in *M. truncatula*	log2Fold-Change	Probable role in symbioses	References
M-type thioredoxin	Medtr2g079400.1	–7.05	Control regulation of bacteroid differentiation in symbiotic nodules	[30]
Membrane steroid-binding protein 1 (MSBP1)	Medtr1g100727.1	–3.17	Negative regulation of brassinosteroid signaling; sterol homeostasis in mycorrhized roots	[31, 32]

Table 3. (Continued)

Gene	Orthologous gene in *M. truncatula*	log2Fold-Change	Probable role in symbioses	References
Component LHCb1/2/3 of LHC–II complex	Medtr4g094605.1	–3.14	Unknown; possible role in plastid functioning in roots	[38]
Component LHCa3 of LHC–I complex	Medtr5g098785.1	–2.38	Unknown; possible role in plastid functioning in roots	[38]
Phytoene synthase (PSY3)	Medtr5g076620.1	–1.53	Catalysis of the first committed and rate-limiting step in carotenoid biosynthesis leads to production of strigolactones	[35]
Plastidial glutamine synthetase (GLN2)	Medtr2g021255.1	–0.93	Carbon metabolism and/or nitrogen assimilation in symbiotic nodules	[33,34]
SMXL strigolactone signal transducer	Medtr4g129230.1	0.99	Suppressor in strigolactone signaling	[39]
Phosphocholine phosphatase	Medtr8g015960.1	1.31	Lipid metabolism in mycorrhizal roots	[40, 41]
Phenylalanine ammonia lyase (PAL)	Medtr1g094780.1	2.05	Flavonoid biosynthesis in roots; possible inhibition of hyphae growth	[42]
4-coumarate: CoA ligase (4CL)	Medtr5g007640.1	2.66	Flavonoid biosynthesis in roots; possible inhibition of hyphae growth	
Contact site protein (VAP27)	Medtr4g027050.1	2.72	Possible role in functional arbuscule development	[43, 44]
Chalcone synthase (CHS)	Medtr5g007713.1	3.26	Flavonoid biosynthesis in roots; possible inhibition of hyphae growth	[45]
Benzyl alcohol O-benzoyltransferase	Medtr0042s0230.1	6.46	Flavonoid biosynthesis in roots; possible inhibition of hyphae growth	[44]

gene in 'high-EIBSM' lines points towards the advantage of plant control of AM fungi spreading over the plant roots.

Some genes were also found to be up-regulated in roots of 'high-EIBSM' lines. Among them is the gene *SMXL* encoding a suppressor of strigolactone signaling [39], which is in line with down-regulated strigolactone biosynthesis characteristic for 'high-EIBSM' lines. Two genes related to mycorrhization were also found to be up-regulated in 'high-EIBSM' lines: the gene encoding phosphocholine phosphatase (probably involved in lipid metabolism that is necessary for AM functioning) and the gene encoding the contact site protein VAP27 (probably participating in membrane structure development during arbuscule formation) [40, 41, 43, 44]. Finally, as many as 4 genes involved in flavonoid biosynthesis, namely *phenylalanine ammonia lyase (PAL), 4-coumarate: CoA ligase (4CL), chalcone synthase (CHS) and Benzyl alcohol O-benzoyltransferase* were found to be up-regulated in roots of 'high-EIBSM' lines. Flavonoids have many functions in roots, as they play a role of signal molecules during the establishment of nitrogen-fixing symbiosis [42] and may also inhibit the growth of fungal hyphae in roots [46]. Since activation of flavonoid biosynthesis may have different outcomes that positively influence plant growth in symbiotic conditions, we can consider the up-regulation of the genes related to flavonoid biosynthesis as an important transcriptome signature inherent to 'high-EIBSM' pea lines. However, further studies are needed to determine the particular role of flavonoid molecules in the efficiency of nitrogen-fixing and AM symbioses.

At least 14 genes encoding transcription factors (TFs) were also identified as up-regulated in the roots of 'high-EIBSM' lines, including the WRKY33 transcriptional regulator, an important marker of pathogen response in plants [47]. It is tempting to speculate that the TFs may play a key role in the formation of the characteristic transcriptome signatures and thus provide the 'high-EIBSM' phenotypic manifestation. Indeed, since the largest proportion (40%–80%) of domestication genes identified so far are transcriptional regulators [48], the TF genes are the primary candidates to be responsible for the quantitative and qualitative differences between pea genotypes using different ecological strategies, namely symbiotic (responsive, or high-EIBSM) and non-symbiotic (non-responsive, or low-EIBSM) strategies of interaction with beneficial soil microorganisms.

CONCLUSION

In this work, the lines previously described as contrasting regarding the EIBSM trait were investigated using transcriptomic analysis. The analysis showed the relatedness of the lines with contrast manifestation of the EIBSM trait, and allowed to determine the differential expression of genes

characteristic for 'high-EIBSM' and 'low-EIBSM' pea genotypes. The results show the principal possibility to investigate the gene expression patterns in genetically diverse, but phenotypically homogenous, groups. By doing so, we managed to highlight the genes, differentiating the high- and low-EIBSM lines, that can be potential expression markers of pea responsivity to inoculation with beneficial soil microorganisms. In general, the overall lower expression of symbiotic genes coupled with the elevated signatures of pathogen response can be the evidence of a stricter control of the plant over its microsymbionts.

DISCLAIMERS

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