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Ginseng including North American ginseng (Panax quinquefolius L.) is one of the most widely used medicinal plants. Its success is thought to be due to a diverse collection of ginsenosides that serve as its major bioactive compounds. However, few genomic resources exist and the details concerning its various biosynthetic pathways remain poorly understood. As the root is the primary tissue harvested commercially for ginsenosides, next generation sequencing was applied to the characterization and assembly of the root transcriptome throughout seasonal development. Transcripts showing homology to ginsenoside biosynthesis enzymes were profiled in greater detail.

RNA extracts from root samples from seven development stages of North American ginseng were subjected to 454 sequencing, filtered for quality and used in the de novo assembly of a collective root reference transcriptome consisting of 41,623 transcripts. Annotation efforts using a number of public databases resulted in detailed annotation information for 34,801 (84%) transcripts. In addition, 3,955 genes were assigned to metabolic pathways using the Kyoto Encyclopedia of Genes and Genomes. Among our results, we found all of the known enzymes involved in the ginsenoside backbone biosynthesis and used co-expression analysis to identify a number of candidate sequences involved in the latter stages ginsenoside biosynthesis pathway. Transcript profiles suggest ginsenoside biosynthesis occurs at distinct stages of development.

The assembly generated provides a comprehensive annotated reference for future transcriptomic study of North American ginseng. A collection of putative ginsenoside biosynthesis genes were identified and candidate genes predicted from the lesser understood downstream stages of biosynthesis. Transcript expression profiles across seasonal development suggest a primary dammarane-type ginsenoside biosynthesis occurs just prior to plant senescence, with secondary ginsenoside production occurring throughout development. Data from the study provide a valuable resource for conducting future ginsenoside biosynthesis research in this important medicinal plant.

Ginseng belongs to species within the genus Panax (family Araliaceae) that comprises approximately 14 species of slow-growing perennial plants with fleshy roots [1]. North American ginseng (Panax quinquefolius L.) is native to eastern North America [2] and Panax species have been used for thousands of years to improve the overall health of human beings, as a remedy to promote vitality, assist the body functions, improve the immune system and protect against stress. It also has been recommended for years as a traditional medicine for a multitude of diseases such as cancer, inflammation, diabetes, cardiovascular ills and obesity [3-7] as well as being a recent source of natural extracts mass marketed as a cold prevention treatment [8].

Ginsenosides are considered to be the major bioactive compounds behind many of the claims of ginseng’s health benefits; they are triterpenoid saponins found nearly exclusively in ginseng and have been the target of considerable research effort [9-11]. To date, more than 150

naturally occurring ginsenosides have been isolated from Panax species and most of them can be classified into two groups based on the skeleton of their aglycones, namely dammarane-type and oleanane-type [12,13]. The dammarane-type consists mainly of three varieties, classified according to their genuine aglycone moieties: 20S-protopanaxadiol (PPD), 20S-protopanaxatriol (PPT), and ocotillol. Rb1, Rb2, Rc, Rd (PPDs) and Re and Rg1 (PPTs) are the most abundant six ginsenosides found in North American ginseng. Over 90% of total ginsenoside content from North American ginseng belongs to these two groups [14,15].

Over the past several years, next-generation sequencing technologies have revolutionized the analysis of genomic information [25]. As applied to the transcriptome with RNAseq, it has been successfully used for transcript profiling, as well as SNP discovery in a number of plant species and has dramatically improved the efficiency and speed of gene discovery [26-28]. The application of 454 next generation sequencing technology has seen a rapid improvement in throughput, read length and accuracy in the past few years, with the GS FLX Titanium server used in this study able to generate one million reads with an average length of 400 bases with 99.5% accuracy [29]. Meanwhile, the analysis of transcriptomic data often relies on aligning reads to a reference which is often not feasible for non-model plant species in which little genomic research has been performed. We applied the transcriptome assembly program Trinity to the assembly of a high quality reference transcriptome for North American ginseng. Trinity has been shown to recover most expressed transcripts as full-length sequences, and is also able to resolve alternative isoforms and duplicated genes, outperforming other de novo assembly tools [30,31]. Our application to ginseng resulted in 41,623 ginseng root transcripts. We fully annotated 84% of these transcripts using sequence similarity searches and protein domain scanning with publicly available databases. In our results, we were able to identify predicted representatives for all of the known enzymes involved in the ginsenoside backbone biosynthesis and also profile their expression levels across seasonal development.

Commercial production of ginseng usually results in harvests after 3 to 5 years. In this study, three-year-old roots were collected, washed, sorted for uniformity and overwintered and grown under simulated growing season conditions in the Biotron facility to minimize variation in environmental factors and soil pathogen infection. Root samples were collected over the fourth-year full growing season at seven development stages [32]: 1) budding - leaf emergence; 2) leaves - distinctive separation of leaf and stem; 3) flowering - plant in full flower; 4) green fruit set; 5) ripe fruit - fruit coloration fully red; 6) fruit drop – including early signs of leaf senescence (e.g., leaf curl) and 7) senescence - complete senescence of leaf and stem (the normal commercial harvest stage) (Figure 1).

Filtering of the sequence data before assembly included steps that removed plastid contaminants and adaptor sequences, as well as trimmed the base pair bias present in the first 15 bp of the 5’ end and low quality bases (Q<30) at the 3’ end. Quality score distributions for reads in each stage before and after filtering are provided in Additional file 2. After filtering, 1,222,382 sequence reads remained for assembly with an average length of 348 base pairs (Table 2). Unfortunately, our poly-A purification step failed to effectively filter the abundant rRNA present and a large percentage of reads had to be filtered from each stage as contaminants arising from ribosomal or plastid RNA sequences. Interestingly, after quality trimming the reads, a disproportionate amount of sequences with lengths of approximately 340 and 410 base pairs were found (Figure 2a). This is presumably an artefact of trends in sequence quality drop off at specific points during sequencing.

To facilitate as complete an annotation as possible for the assembly, sequence similarity searches [33] were performed against a collection 5,018 Ginseng ESTs from GenBank, the Arabidopsis genome (TAIR10), the uniProt Plant Protein Annotation Program (PPAP) database and GenBank’s non-redundant (nr) protein database. In addition, protein domain scanning using hidden Markov models (HMMs) from Pfam were applied as well as the assignment of metabolic pathway information from the Kyoto Encyclopedia of Genes and Genomes (KEGG) database. Overall, these efforts annotated 83.6% of transcripts in the assembly.

As Arabidopsis is the most thoroughly annotated plant, sequence homology to Arabidopsis was also used to characterize the transcriptome based on Gene Ontology (GO) information. GO annotation provides descriptions of gene products in terms of their associated molecular functions, cellular components, and biological processes. Using sequence homology to TAIR10, 14,537 GO terms were assigned to 24,110 sequences categorized into 80 functional groups. GO assignments were most frequently related to biological processes (6,431), followed by cellular components (12,489) and molecular function (5,190) (Figure 4).

The assembly was scanned with protein domain HMM models from the Pfam database in order to catalogue any significant matches (E<e-10) to known protein domains. Overall, 32,277 HMMs were scanned against the assembly resulting in annotation for 21,263 transcripts possessing 17,266 different protein domains. This added annotation information to an additional 77 transcripts that had no hits in the prior homology searches. The most abundant domain found was the protein kinase domain, present in 1,310 transcripts. This is a similar number to the 1,719 kinases present in the Arabidopsis genome and not surprising, as protein kinases play a role in a multitude of cellular processes, including division, proliferation, apoptosis, and differentiation.

Finally, in order to assign metabolic information to our transcripts, the KAAS tool (http://www.genome.jp/tools/kaas/)[34] was used to assign pathway information from the KEGG database. This resulted in a KEGG orthology (KO) number for 5,717 transcripts that possessed homology with metabolic enzymes in the KEGG database. The pathways most strongly represented in the results were protein processing in the endoplasmic reticulum, ubiquitin mediated proteolysis, nucleotide excision repair, arginine and proline metabolism, peroxisome, amino sugar and nucleotide sugar metabolism, proteasome, starch and sucrose metabolism and glycolysis/gluconeogenesis. All annotation information and significance scores were summarized and concatenated with transcript identifiers into a single line of annotation for each sequence in a Fasta formatted transcriptome file (Additional file 3).

To evaluate the contribution of each stage of development to the reference transcriptome and profile the relative expression levels of transcripts throughout development, we mapped all high quality reads from each stage back to the assembled transcriptome using the BWA tool [35]. While this is useful in determining relative transcript abundance, it did have the unfortunate side effect of reporting unmapped reads for 6,113 transcripts. Investigating further, it was found that nearly all unmapped transcripts were involved in alternative splicing and of the shortest transcripts in the assembly (mean length: 414 bp). We presume that this is a consequence of the k-mer (k=25) assembly process used by Trinity, perhaps creating isoform transcripts that are shorter than the long 454 reads from which they originally derive or possibly from read trimming by the alignment program. Nevertheless, expression information was obtained for over 85% of the transcriptome which comprised the longer contigs.

Counts for mapped reads were then used to generate RPKM (reads per kilobase transcript per million reads mapped) values for each putative transcript in each developmental stage. Of the most abundantly expressed predicted proteins, storage proteins topped the list, with a number of Panax ginseng annotated proteins: RNase-like major storage protein, specific abundant protein, tonoplast intrinsic protein, major latex-like protein and dehydrin 4 (Table 3).

We also examined the level of overlap in transcript expression occurring between major developmental stages of the plant. To limit the complexity in the number of comparisons needed, the seven developmental stages sampled were grouped into the broader developmental categories of budding (stages 1/2), flowering (stage 3), fruiting (stages 4/5) and senescence (stages 6/7). Overall, 26,681, 17,990, 26,162 and 26,772 predicted transcripts showed positive expression in each category respectively. Each category possessed around two thousand predicted transcripts uniquely expressed during that stage of root development, with the exception of flowering, which had 621 specific transcripts. However, this is likely influenced by the fact that flowering is the only single stage group and thus represents a snapshot from a shorter period of developmental time compared to the other stages. Interestingly, the senescence stage had the largest number of predicted transcripts overlapping with other developmental stages. Altogether, a total of 13,074

transcripts were found to be expressed throughout all stages of development (Figure 5).

As ginsenosides are the ultimate compound of commercial interest in ginseng harvest, we sought to inventory all putative transcripts in the assembly that could be implicated in the synthesis of ginsenosides and examine their expression profiles across seasonal development. We therefore took all KEGG orthology numbers associated with enzymes in the mevalonate pathway of terpenoid backbone biosynthesis along with those from the sesquiterpenoid and triterpenoid biosynthesis pathways leading to chair-chair-chair-boat conformation triterpenoids (of which ginsenosides belong) and pulled all transcripts annotated with corresponding KO numbers in the assembly. This returned 14 predicted genes (43 transcripts including isoforms) annotated and identified by KEGG orthology. In addition, as there was no appropriate assigned KEGG EC for β-amyrin synthase, five β-amyrin synthase annotated genes (6 transcripts including isoforms) were pulled for analysis using homology annotation in the assembly (Table 4).

In North American ginseng, the majority of ginsenosides are known to be of the dammarene-type ginsenosides produced from protopanaxdiol and protopanaxtriol triterpenes. Dammarenediol-II produces protopanaxdiol and protopanaxtriol, and ginsenosides are thought to be synthesized from subsequent hydroxylation of these products by cytochrome P450 enzymes and glycosylation by glycosyltransferases (GTs) [22-24]. Our assembly contained 175 predicted transcripts annotated as Cytochrome P450s; with 63 of these possessing high similarity to P450 sequences from Panax ginseng and Panax notoginseng EST collections. Similarly, the assembly contained 164 predicted transcripts annotated as glycosyltransferases with 54 of these previously identified in Panax ginseng, Panax notoginseng and Panax quinquefolias. In order to identify potential candidates from these gene families that may be functioning in the latter stages of ginsenoside biosynthesis, we conducted a co-expression analysis with the transcript profiles for our putative dammarenediol synthase (DS) and squalene expoxidase (SQE) found immediately upstream in the ginsenoside biosynthesis pathway.

In order to provide biological validation to the 12 predicted transcripts showing coexpression with our putative DS gene, we conducted real-time PCR against the DS gene itself, the 6 putative glycosyltransferase genes and 6 putative cytochrome P450 genes across the final 3 stages of development. We were able to successfully amplify all 13 genes using RT-PCR analysis and confirmed strong coexpression between our predicted DS, 5 of the glycosyltransferase transcripts and 4 of the P450 transcripts (Figure 6). Additional file 4 lists the primers used in this analysis.

Before examining the relative expression profiles of our identified biosynthesis genes we sought to first look at the expression profiles for the entire transcriptome across seasonal development. RPKM values for all predicted transcripts were thus hierarchically clustered, and displayed in a heat map to create a transcriptome-wide display of developmental expression (Figure 7a). Many transcripts showed maximum expression within one or two specific stages of root development relative to other stages, with all stages of development possessing distinct clusters of genes showing dominant expression within that stage. Moreover, compared to other stages of development, senescence possessed a disproportionately large cluster of transcripts exhibiting a senescence-specific maximum in expression.

Expression profiles for all predicted genes and their isoforms implicated in ginsenoside biosynthesis (Figure 7b) as identified above were also hierarchically clustered and plotted in a heat map (Figure 7c). For representatives of downstream candidates, the most highly co-expressed P450 and glycosyltransferase transcripts identified in the co-expression analysis were also included in the collection. As seen with the entire transcriptome, many enzymes displayed abundant expression, specific to one or a few developmental stages relative to the other stages. To our surprise, stage 3 (Flowering) and stage 6 (Fruit drop) both possessed obvious clusters that encompassed putative representatives for almost all the enzymes in the biosynthesis pathway, suggesting that these two developmental stages are important points of ginsenoside biosynthesis in the developing plant. In the case of stage 7, this makes intuitive sense considering the traditional time of ginseng harvest after the fruit drop stage and onset of leaf senescence. Interestingly, when different isoforms of genes were present, they tended to exhibit expression maxima in different stages of development.

This was most apparent with the 9 different isoforms of SQE1 (Pq7190), for which at least one instance of an isoform with stage specific expression was found in all developmental stages except senescence stage 7 (Figure 7c). Of course, due to the computational limitations of assembly and mapping, both the isoforms identified and the expression profiles should be interpreted with caution without further in planta validation.