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Review

Omics studies of citrus, grape and rosaceae fruit trees

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Recent advance of bioinformatics and analytical apparatuses such as next generation DNA sequencer (NGS) and mass spectrometer (MS) has brought a big wave of comprehensive study to biology. Comprehensive study targeting all genes, transcripts (RNAs), proteins, metabolites, hormones, ions or phenotypes is called genomics, transcriptomics, proteomics, metabolomics, hormonomics, ionomics or phenomics, respectively. These omics are powerful approaches to identify key genes for important traits, to clarify events of physiological mechanisms and to reveal unknown metabolic pathways in crops. Recently, the use of omics approach has increased dramatically in fruit tree research. Although the most reported omics studies on fruit trees are transcriptomics, proteomics and metabolomics, and a few is reported on hormonomics and ionomics. In this article, we reviewed recent omics studies of major fruit trees, i.e. citrus, grapevine and rosaceae fruit trees. The effectiveness and prospects of omics in fruit tree research will as well be highlighted.

Key Words: citrus, grapevine, metabolomics, omics, proteomics, rosaceae fruit tree, transcriptomics.

Introduction

In the last two decades, comprehensive studies called omics, have been applied on model plant study and has contributed enormously in plant science. The conceptual scheme of "omics" is described in **Fig. 1**. Genome means a full haploid set of chromosomes with its gene set in one organism whereas phenome is the physical appearance (phenotype) of an organism. Transcriptome and proteome respectively describes the entire set of RNAs and proteins derived from genome. Metabolome, hormonome and ionome are all metabolites, hormones and ions present in a biological sample, such as a cell, tissue, organ or organism, respectively. Comprehensive analysis targeting genome, transcriptome, proteome, metabolome, hormonome, ionome and phenome are called genomics, transcriptomics, proteomics, metabolomics, hormonomics, ionomics and phenomics, respectively. Recently, combination and integration of several omics are performed on a single sample or material and these are called multi-omics or integrated-omics. The advance of omics study is supported by the invention and improvement of analytical instruments, including next generation DNA sequencer (NGS) and mass spectrometer (MS). Omics data are analyzed by the use of bioinformatics and various important genes, proteins, metabolites and metabolic pathways have been identified by these approaches.

For the model plant, Arabidopsis, a precise genome sequence data and gene prediction with substantial annotations are provided and a vast omics data, especially transcriptome, proteome and metabolome data have been collected in databases. On the contrary, availability of this information is limited for horticultural crops. The recent decrease in cost of DNA sequencing has made it possible to sequence various crop genomes as well as making transcriptome data more available and accessible. In addition, proteomics and metabolomics are often applied in various crop studies these days.

Every fruit has a unique and attractive characteristic, i.e. taste, flavor, color, shape and texture. Clarification of fruit developmental physiology, metabolic pathways and identification of key genes of important traits are necessary to improve fruit yield and quality. Fruit trees studies have many disadvantages; such as long juvenility (long life cycle), heterosis, self-incompatibility, polyploidy, large body size (require large cultivation space). Due to these disadvantages, fruit tree research is far less advanced compared to herbaceous crops. These have also hindered comprehensive research activities on fruit tress thereby leaving a vast number of undiscovered genes, metabolites, metabolic pathways and physiological activities in fruit trees. Omics study is the powerful approach that has been used recently by researchers to overcome these shortcomings. In this article, we review recent omics studies in fruit tree research.

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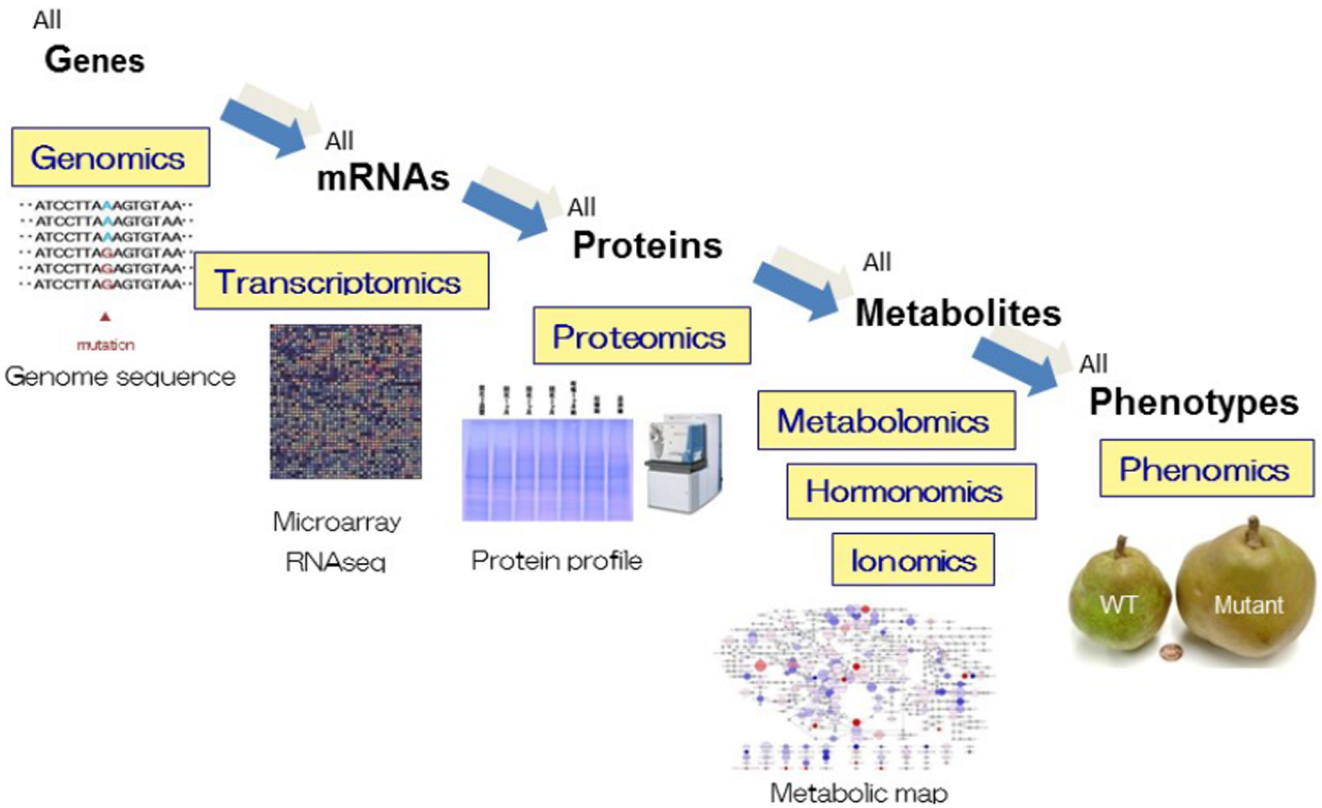

Fig. 1. Conceptual scheme of omics study. Comprehensive studies targeting all genes, transcripts (RNAs), proteins, metabolites, hormones, ions and phenotypes are called genomics, transcriptomics, proteomics, metabolomics, hormonomics, ionomics and phenomics, respectively.

Genomics

Development of NGS and technology for assembly of sequence data from NGS has made whole genome sequencing of horticultural crops possible. In 2007, grapevine genome was sequenced firstly in fruit trees and fourthly in plants, i.e. after Arabidopsis, rice and poplar (Jaillon *et al.* 2007). Nowadays genomes of some horticultural crops, including apple, peach, Japanese apricot, Chinese pear, Valencia orange, mandarin orange, and had already been sequenced (http://www.genome.jp/kegg/catalog/org_list.html). As shown in **Table 1**, the genome data of rosaceae plants, citrus and grapevine are released from several databases. Comparison of genome sequences among different cultivars is an effective approach to identify genes for cultivar-specific traits. One interesting example is the report by Da Silva *et al.* (2013). That is, they compared genome sequences between 'Pinot Noir' and 'Tannat', and found cultivar-specific genes, which contribute to a high accumulation of polyphenolic compounds in Tannat grape berry. In addition to *de novo* sequencing of genomes of horticultural crops, resequencing of genomes of different cultivars is a promising approach.

Transcriptomics

Transcriptomics is the comprehensive study of transcripts, i.e. RNAs, in an organism, organ, tissue or cell. Microarray, also called gene chip or DNA chip was the most popular tool to perform transcriptome analysis. To design microarray, information of predicted genes from genome sequence or expressed sequenced tag (EST) is required. For minor crops, neither genome sequence nor EST is available to design its microarray. However, recently the situation has changed. By the invention of NGS and advance of bioinformatics, RNA sequencing (RNAseq) became a popular approach in transcriptomics. More than 10 million sequence reads from NGS are assembled using reference sequence, such as genome sequence or EST, or *de novo*. From the number of sequence reads for one gene, its expression level is calculated. In case of *de novo* assembly, no reference sequence is required; therefore it can be applied on organisms without genome sequence data and EST. Most publications reporting transcriptomics of fruit trees after 2014 used RNAseq (**Supplemental Table 1**). In fruit trees, there are various target traits for transcriptomics and the major ones are gene expression profile in different tissues and organs, fruit development, ripening and post-harvest physiology, fruit traits (size, color, brix, acidity, firmness, flavor), secondary metabolites (anthocyanin, carotenoid) and response to pathogens, stresses or plant hormones.

Table 1. Useful web pages for fruit omics study

Name	Object	Target/Species	URL
Genome Database for Rosaceae	genome	rosaceae plants	https://www.rosaceae.org/
Citrus Genome Database	genome	citrus	https://www.citrusgenomedb.org/
Grape Genome Database	genome	grape	http://genomes.cribi.unipd.it/grape/
Grape Genome Browser	genome	grape	http://www.genoscope.cns.fr/externe/GenomeBrowser/Vitis/
PlantGDB	genome	various plants (grape, peach, papaya)	http://www.plantgdb.org/
GEO	microarray raw data	all organisms	http://www.ncbi.nlm.nih.gov/geo/
SRA	RNAseq raw data	all organisms	http://www.ncbi.nlm.nih.gov/sra
eFP Browser	gene expression	various plants (grape)	http://bar.utoronto.ca/efp_grape/cgi-bin/efpWeb.cgi
ATTED-II	coexpression	various plants (grape)	http://atted.jp/
CoP	coexpression	various plants (grape)	http://webs2.kazusa.or.jp/kagiana/cop0911/
MassBank	MS spectrum	all metabolites	http://www.massbank.jp/index.html?lang=en
ReSpect	MS spectrum	all metabolites	http://spectra.psc.riken.jp/
KNApSAcK	metabololite	all metabolites	http://kanaya.naist.jp/KNApSAcK_Family/
KEGG	metabolic pathway etc.	various organisms (grape)	http://www.genome.jp/kegg/
PMN/PlantCyc	metabolic pathway	various plants (grape, papaya)	http://www.plantcyc.org/
VitisCyc	metabolic pathway	grape	http://pathways.cgrb.oregonstate.edu/index.html
KaPPA-View 4 KEGG	metabolic pathway drafting	various plants (grape)	http://kpv.kazusa.or.jp/kpv4-kegg-1402/
Fruit Omics Database	omics data	fruit trees (pear)	http://www.tr.yamagata-u.ac.jp/~oikawa/oikawa/GLPDB%202/GLPDB_E/index.html

Citrus

Several transcriptomics of citrus focusing on citrus greening (huanglongbing (HLB)) disease have been reported (Mafra *et al.* 2013, Martinelli *et al.* 2012, 2013) together with combination of proteomics (Fan *et al.* 2011, Zhong *et al.* 2015). HLB disease is one of the serious diseases in citrus cultivation and there is no effective countermeasure against this disease. Although the key gene for HLB resistance has not been identified yet, many candidates and regulated genes have been found in these omics studies. To clarify self-incompatibility mechanism, Zhang *et al.* (2015c) performed RNAseq in lemon and found a putative S-RNase gene that had not been previously reported. Transcriptome and proteome analyses of a spontaneous late-ripening sweet orange mutant were performed (Wu *et al.* 2014b, Zeng *et al.* 2012, Zhang *et al.* 2014b). From these omics studies, the presence of multiple ripening events in citrus or roles of abscisic acid (ABA), sucrose and jasmonic acid (JA) in citrus ripening was suggested. Sun *et al.* (2012) and Zhang *et al.* (2011a) reported transcriptomics and Ai *et al.* (2012) reported multi-omics (transcriptomics and proteomics) data on an early flowering tyrifoliate orange mutant. The target of transcriptomics in Sun *et al.* (2012) was not mRNA but microRNAs (miRNAs), which are small non-coding RNAs (ncRNAs) that regulate RNA silencing and post-transcriptional genes regulation. RNAseq using NGS is the major approach to analyze ncRNA comprehensively. Nishikawa *et al.* (2010) performed microarray analysis for the early flowering transgenic tyrifoliate orange expressing *Flowering Locus T* from citrus (*CiFT*) and confirmed higher gene expression levels of MADS-box transcription factors related to floral organ formation.

Corky split vein is caused by boron deficiency. Yang *et al.* (2013) and Lu *et al.* (2014) reported transcriptomics for boron deficiency in citrus. The former study suggested the involvement of cytokinin signaling pathway in corky split vein. On the other hand, the latter study focused on miRNAs and suggested the involvement of miRNAs in the response to boron deficiency. Recently, single cell omics has become a trend in biology. Voo and Lange (2014) reported a protocol for the isolation of essential oil gland cells of citrus fruit peel for single cell transcriptomics. Transcriptomics of citrus focusing on physiological abscission of fruits, called "self-pruning" (Zhang *et al.* 2014a), polyploidy (Allario *et al.* 2011), somatic hybrid (Bassene *et al.* 2010), response to ethylene in fruit (Patel *et al.* 2014) or GA treatment on bud (Goldberg-Moeller *et al.* 2013), red fruit flesh (Bernardi *et al.* 2010, Yu *et al.* 2012), fruit skin color (Guo *et al.* 2015) and flavor (Tietel *et al.* 2011) also have been reported (**Supplemental Table 1**).

Grapevine

Fasoli *et al.* (2012) performed a large scale transcriptome analysis of grapevine. This study determined transcriptomes of 54 samples for various tissues and organs at different developmental stages. The obtained transcriptome data have been registered in eFP Browser (see the chapter "Omics Databases and Tools") to be used as a valuable tool. Interestingly co-expression analysis of the transcriptome data revealed "woody developmental program", which is a characteristic of perennial woody plants, and is inactive in vegetative/green tissues in grapevine. Many transcriptomics of grapevine focused on response to pathogens, including fungus, oomycete, virus and phytoplasma (Abbà *et al.* 2014, Almagro *et al.* 2014, Gauthier *et al.* 2014, Giraud *et al.* 2012, Li *et al.* 2015, Malacarne *et al.* 2011, Vega

et al. 2011). Gray mold caused by *Botrytis cinerea* is one of the most problematic diseases of grapevine. To clarify the resistance mechanism against *B. cinerea*, multi-omics approaches, such as transcriptomics, proteomics (Dadakova *et al.* 2015), and metabolomics (Agudelo-Romero *et al.* 2015), were performed. The latter study provided evidence of a reprogramming of carbohydrate and lipid metabolisms towards synthesis of secondary metabolites involved in plant defense, including resveratrol. The other transcriptomics studies also revealed dynamic changes in gene expressions upon pathogens infection.

Another major targets of grapevine transcriptomics are ripening of berry (Carbonell-Bejerano *et al.* 2013, Guillaumie *et al.* 2011, Koyama *et al.* 2010, Lijavetzky *et al.* 2012) and syntheses of ripening related secondary metabolites, such as anthocyanins (Ali *et al.* 2011, Wu *et al.* 2014a), proanthocyanidins (Carrier *et al.* 2013) and volatile compounds (Cramer *et al.* 2014). Contents of anthocyanins, proanthocyanidins and volatile compounds decide color, taste and flavor of grape berry and wine, respectively. Dramatic increase of ABA in the later berry growth is a trigger of ripening and this stage is called "véraison". Several studies have reported the relationship between ABA, ripening and anthocyanin accumulation (Carbonell-Bejerano *et al.* 2013, Koyama *et al.* 2010). On the other hand, Cramer *et al.* (2014) reports the relation between ethylene signaling and flavor synthetic pathway in berry skin at ripening stage. Another important plant hormone in grape berry growth is gibberellin (GA). The first exogenous application of GA on grape flowers induces seedless fruits and the second application (about 10 days after flowering) induces parthenocarpic fruit set. Transcriptome analyses in grape berries after GA application (Chai *et al.* 2014, Cheng *et al.* 2015) and in seedless somatic variant (Nwafor *et al.* 2014) have been performed. The transcriptomics by Chai *et al.* (2014) revealed that exogenous GA induced cross talk between auxin, cytokinin, brassinosteroid (BR), ABA and ethylene. Some transcriptomics of grapevine focus on environmental conditions and stresses, such as different growing areas "*terroir*" (Dal Santo *et al.* 2013, Sun *et al.* 2015), cold (Xin *et al.* 2013), heat (Rocheta *et al.* 2014), drought (Corso *et al.* 2015, Perrone *et al.* 2012), salt (Daldoul *et al.* 2010) stresses and high light intensity (Carvalho *et al.* 2011). Other transcriptomics of grapevine focus on different species (Wen *et al.* 2013), tendril and inflorescence development (Díaz-Riquelme *et al.* 2014), defoliation (Pastore *et al.* 2013), bud dormancy (Díaz-Riquelme *et al.*2012), graft union formation (Cookson *et al.* 2013), late harvest technique (Corso *et al.* 2013), pest damage (Nabity *et al.* 2013) and so on (**Supplemental Table 1**).

Rosaceae fruit trees

Peach, cherry, apricot, apple and pear belong to Rosaceae family. Peach, cherry and apricot are called stone fruits, because the fruit has a large and hard seed, and their fruit flesh is derived from pericarp (mesocarp). Whiles apple and pear belong to pome fruits and their fruit flesh is derived from receptacle. Therefore transcriptomes, proteomes and metabolomes of stone fruits and pome fruits might be different. One of the major targets of transcriptomics of rosaceae fruit trees is response to pests, such as infection of fungi (Gusberti *et al.* 2013) or virus (Chen *et al.* 2014) in apple, infection of bacteria (Socquet-Juglard *et al.* 2013) or virus (Herranz *et al.* 2013, Rubio *et al.* 2015) in peach, virus infection in plum (Rodamilans *et al.* 2014) and insect damage in apple (Zhang *et al.* 2015b). In these studies, induction of known and unknown genes expressions related to pest resistance was detected. In Gusberti *et al.* (2013), several candidate genes involved in the ontogenic resistance of apple were identified. Most rosaceae fruit trees need cumulative chilling in winter to break bud dormancy in spring. Transcriptomics targeting bud dormancy of Japanese pear (Bai *et al.* 2013, Liu *et al.* 2012, Nishitani *et al.* 2012a), Chinese cherry (Zhu *et al.* 2015) and peach (Barakat *et al.* 2012) have been reported. Interestingly, transcriptomics both by Bai *et al.* (2013) and Nishitani *et al.* (2012a) revealed decrease in gene expressions for ABA and GA biosynthesis, down-regulation of dormancy-associated MADS-box gene and involvement of epigenetic regulation during endodormancy release. Tree architecture is an important trait in orchard management. One of the characteristic tree architecture of apple is "columnar". Krost *et al.* (2012, 2013) performed transcriptome analyses for columnar apples. They couldn't find the causative gene of columnar, but their transcriptomics provided a molecular explanation for earlier findings on the hormonal state of columnar apple trees.

Abscission of fruits is one of the important traits in fruit tree cultivation. Ferrero *et al.* (2015) performed transcriptomics of young seeds and discussed its relation to physiological abscission of apple fruits. Zhu *et al.* (2011) focused on abscission of apple fruits induced by application of a synthetic auxin analogue, naphthaleneacetic acid (NAA). Nishitani *et al.* (2012b) compared transcriptomes among various parthenocarpic genetic resources of pear and found several phenylpropanoid-related and photosystem-related genes as differently expressed genes. The authors suggested that these genes might be candidates DNA markers for parthenocarpy. Nashima *et al.* (2013a) performed transcriptome analysis throughout fruit development of European pear and the data is released from "Fruits Omics Database" (**Fig. 2**). The transcriptome data revealed the dynamic fluctuations of gene expressions during fruit development, including high expression of genes related to stone cell formation at early fruit developmental stages and those related to ripening at ripening stage. Xie *et al.* (2013) reported transcriptome analysis of Chinese pear and also showed dynamic fluctuations of gene expressions during fruit development. Many transcriptomics studies of rosaceae fruit trees focused on fruit ripening and postharvest physiology, such as in apple (Costa *et al.* 2010, Gapper *et al.* 2013, Mellidou *et al.* 2014), peach (Falara *et al.* 2011, Lauxmann *et al.*

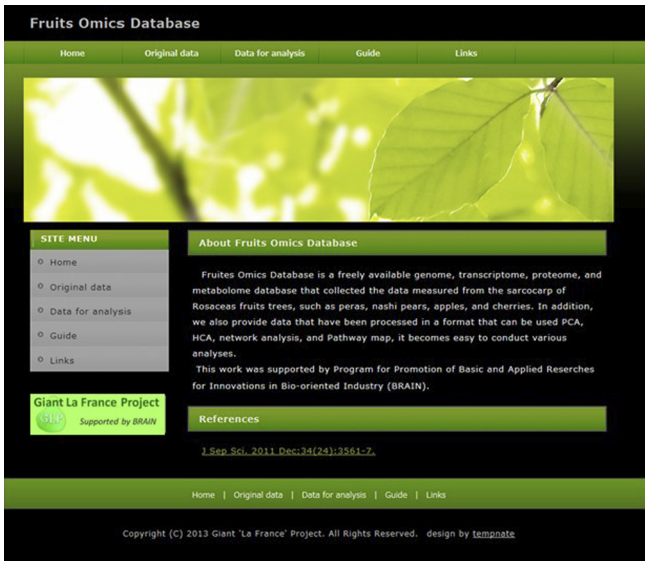

Fig. 2. "Fruits Omics Database". The website, named "Fruits Omics Database", are collecting transcriptome, proteome, metabolome, hormonome and ionome data of fruits, especially focusing rosaceae fruit trees. At present, the transcriptome, metabolome, hormonome and ionome data of European pear fruits are available. The URL of Fruits Omics Database is http://www.tr.yamagata-u.ac.jp/~oikawa/oikawa/GLPDB%202/GLPDB_E/index.html.

2012, Pons *et al.* 2014) and Chinese pear (Huang *et al.* 2014, Liu *et al.* 2013). To prolong storage period of apple fruits, controlled atmosphere (CA) storage and a competitor of ethylene receptor, 1-methylcyclopropene (1-MCP), treatment are applied in the apple industry. Mellidou *et al.* (2014) focused on CA storage, Costa *et al.* (2010) focused on 1-MCP treatment and Gapper *et al.* (2013) focused on both. Interestingly, Huang *et al.* (2014) and Gapper *et al.* (2013) suggested the involvement of epigenetic regulation during fruit ripening and storage.

Schaffer *et al.* (2013) or Wu *et al.* (2015) compared transcriptomes between normal apple cultivar and its transgenic plants of the MADS box gene, *SEP1/2*, or the gene encoding the key enzyme for sorbitol synthesis, aldose-6-phosphate reductase (A6PR), respectively. Many other traits of rosaceae fruit trees have been studied by transcriptomic approach. Several transcriptomics studies focused on stress resistances, such as cold (Mousavi *et al.* 2014, Puig *et al.* 2015), drought (Wang *et al.* 2015) and salt (Li *et al.* 2013) stresses. Li *et al.* (2012) determined differences between Japanese apricot and apricot transcriptomes. Similarly, Wei *et al.* (2015) compared difference in transcriptomes between yellow peel and red peel cultivars of cherry, whereas Vimolmangkang *et al.* (2014) compared difference in transcriptomes in apple skin between in light and dark conditions. Further transcriptome studies will clarify interesting traits of rosaceae fruit trees, such as species- or cultivar-specific traits and a unique sugar metabolism, i.e. sorbitol metabolism, in Rosaceae fruit trees.

Proteomics

Proteomics is the comprehensive study of proteins in an organism, organ, tissue or cell. Peptide sequencing, i.e. Edman sequencing, was the popular method to identify proteins before. However nowadays MS is used for protein identification and quantification in almost all proteomics. To identify proteins by MS, protein sequence database is required. Protein sequence database of allied species or other organisms can be used. However, for efficient and accurate identification, protein sequence database derived from one's own genome sequence or EST should be available for usage. Normally number of proteins identified in one proteomics is less than 10% of gene number, because of the sensitivity of MS and masking of minor peptides by major ones.

Before MS analysis, proteins are often separated, enriched or labeled depending on purposes. In comparative proteomics, 2D-PAGE are often used. Comparing several 2D-PAGE images, difference in protein amounts among different samples can be determined. iTRAQ labeling is also one of the methods in comparative proteomics (Bindschedler and Cramer 2011) and various studies of fruit trees have used iTRAQ labeling (Ai *et al.* 2012, Fan *et al.* 2011, Hu *et al.* 2015, Palmieri *et al.* 2012, Wu *et al.* 2014b, Zheng *et al.* 2014, Zhong *et al.* 2015, Zhou *et al.* 2015). Post translational modifications of proteins, such as acetylation, glycosylation and phosphorylation, can be monitored in proteomics. Protein phosphorylation often causes dynamic change in protein function. Therefore, to identify phosphorylation status of proteins, phosphoproteomics is performed. Phosphoproteomics has also been used in fruit tree proteomics (Margaria *et al.* 2013, Wang *et al.* 2014, Zeng *et al.* 2014) (**Supplemental Table 1**). Concerning proteomics of fruit trees, one review article has been published (Molassiotis *et al.* 2013).

Citrus

By proteomic approach, Katz *et al.* (2010) identified approximately 1,500 proteins in citrus fruit juice sac cells and quantified their amounts at three developmental stages. As a protein database for this proteome analysis, a comprehensive sequence database of citrus genes, ESTs and proteins, named iCitrus, has been established. Peel color of citrus fruit changes from green to yellow or orange during fruit maturation. The green color is derived from chlorophyll in chloroplast and chloroplast change to chromoplast accumulating carotenoids during fruit maturation. Zeng *et al.* (2011) identified 493 proteins in sweet orange, including proteins involved in carotenoid synthesis and storage in the chromoplast. Comparison of chromoplast proteomes between sweet orange and tomato showed some unique characteristics of the sweet orange chromoplast. The sweet orange chromoplast has more extensive carotenoid synthesis and amino acid synthesis without nitrogen assimilation and lipid metabolism for jasmonic acid (JA) synthesis.

Phosphoproteomics of chromoplast for sweet orange have been performed and 109 plastid-localized phosphoproteins were identified during fruit ripening (Zeng *et al.* 2014). This shows the existence of active protein regulation via post-translational modifications in the chromoplast. These organelle proteomics showed interesting characters of chromoplast in fruits.

Many citrus species show "biennial bearing", also called "alternate bearing", meaning repeating heavy fruit load (on-crop) and low yield (off-crop) in every other year. To clarify the mechanism of biennial bearing, 2D-PAGE images of on-crop and off-crop were compared and then the differentially expressed proteins were identified by proteomic approach (Muñoz-Fambuena *et al.* 2013a, 2013b). The results showed that the proteins involved in the primary metabolisms, such as carbohydrate metabolism, were more abundant in the buds and leaves of off-crop trees. Shalom *et al.* (2014) compared transcriptomes of buds between on-crop and off-crop trees. The result revealed up-regulation of genes involved in photosynthesis and ABA metabolism and down-regulation of auxin polar transport in off-crop trees, although their hormone analyses showed the decrease of both ABA and auxin levels in the buds of off-crop trees. Additionally, proteomics of citrus focusing on response to male sterility (Zheng *et al.* 2014), response to pathogens (Dória *et al.* 2015, Monavarfeshani *et al.* 2013, Nwugo *et al.* 2013, Rani and Podile 2014, Rani *et al.* 2015), pest damage and methyl JA treatment (Maserti *et al.* 2011), water deficit (Oliveira *et al.* 2015), salt stress (Podda *et al.* 2013, Tanou *et al.* 2014) and Fe (Muccilli *et al.* 2013) and Mg (Peng *et al.* 2015) deficiencies have been also reported (**Supplemental Table 1**).

Grapevine

Many proteomics of grapevine focused on response to pathogens (Belchí-Navarro *et al.* 2013, Dadakova *et al.* 2015, Margaria *et al.* 2013, Palmieri *et al.* 2012, Spagnolo *et al.* 2012, 2014, Yao *et al.* 2012, Zhao *et al.* 2011). In these studies, proteins related to defense response, including pathogenesis related (PR) proteins and proteins involved in signal transduction of defense response, were identified. Yao *et al.* (2012) studied Mn-induced resistance against powdery mildew in grapevine. Their proteome analysis showed induction of PR-like protein and nucleotide-binding site-leucine-rich repeat (NBS-LRR) proteins, which detect pathogens. This suggests that high concentration of Mn triggers defense mechanisms against pathogens in grapevine. Margaria *et al.* (2013) performed phosphoproteomics in grapevine leaves after phytoplasma infection. In the phosphoproteomics, 15 differentially phosphorylated proteins of healthy and infected plants, including proteins involved in response to stress and antioxidant system, were identified. This shows importance of protein phosphorylation for defense response. One of the interesting reports is the proteomics of grape embryogenic callus in the response to *Agrobacterium tumefaciens*-mediated transformation (Zhao *et al.* 2011). PR10 and resistance protein Pto were identified as proteins significantly up-regulated after *A. tumefaciens* inoculation. In addition, by biochemical measurements, *A. tumefaciens* transformation induced oxidative burst and modified protein-degradation pathways. The authors suggested that the apoptosis signaling pathway and hypersensitive response are strengthened by *A. tumefaciens* transformation and these partially explain the low efficiency of grape transformation. Regarding interaction between grapevine and microorganisms, proteomes of non-mycorrhizal and mycorrhizal roots of grapevine were analyzed (Cangahuala-Inocente *et al.* 2011).

Concerning grape berry ripening, Negri *et al.* (2011) detected 36 proteins, which amounts changed significantly after véraison, by proteomic approach. Most of them were related to biotic and abiotic stress responses. Thus the authors suggested that such proteins involved in biotic and abiotic stress responses must be most significant biomarkers for berry ripening. Zamboni *et al.* (2010) performed thorough multi-omics, i.e. a combination of transcriptomics, proteomics and metabolomics, during berry development and postharvest drying "withering". In this study, the authors identified stage-specific biomarkers for berry development and withering. Metabolomes in berries between red and white grapes (Niu *et al.* 2013b), among different varieties (Bertazzo *et al.* 2010), among different *terroir* and ripening stages (Fraige *et al.* 2015) have been compared. Other proteomics of grapevine focused on postharvest withering (Di Carli *et al.* 2011), thermal stresses (George *et al.* 2015) and light (Nilo-Poyanco *et al.* 2013, Niu *et al.* 2013a) (**Supplemental Table 1**).

Rosaceae fruit trees

Long juvenility is a problematic trait in fruit tree cultivation and breeding. Zeng *et al.* (2010) and Cao *et al.* (2011) compared proteomes among juvenile, adult vegetative and reproductive phases in apple. The former report concluded that the transition from vegetative phase to reproductive phase is regulated independently. Bud dormancy is also another problematic trait in fruit tree cultivation in warm area and it is becoming more severe because of global warming. Zhuang *et al.* (2013) compared proteomes of dormant buds of Japanese apricot at four stages and similarly, vegetative buds and floral buds of peach in post-dormancy were compared by Prassinos *et al.* (2011). They identified many differentially expressed proteins which may be related to bud dormancy and its release. Self-incompatibility is also another problematic trait in fruit tree cultivation and breeding. Cao *et al.* (2012) compared proteomes in primary styles of self-incompatible and compatible apricots and found differentially expressed proteins.

Hu *et al.* (2011) performed proteome analysis of peach endocarp (stone) and mesocarp (fruit flesh) during early fruit development. They found higher expression of enzymes involved in lignin and flavonoid synthetic pathways in the endocarp. Transcriptomes and proteomes of European

pear fruits throughout its development were determined by Nashima *et al.* (2013a) and Reuscher *et al.* (2016), respectively. In these studies, higher expression of enzymes involved in lignin and flavonoid synthetic pathways in early developmental stages was revealed. The higher expression of enzymes involved in lignin and flavonoid synthetic pathways might be responsible for stone hardening in peach and stone cell formation in pear. Fruit firmness is one of the important traits of fruits. Marondedze and Thomas (2012) compared proteomes of high and low fruit firmness of apple cultivars. The result indicated a lower expression of proteins involved in ethylene biosynthesis in the high firmness cultivar. Several proteomic works for rosaceae fruit trees have focused on fruit ripening and postharvest physiology, which includes; fruit ripening of apricot (D'Ambrosio *et al.* 2013), fruit softening in melting peach varieties (Nilo *et al.* 2012), postharvest heat treatment of peach fruits (Bustamante *et al.* 2012, Jiang *et al.* 2014, Zhang *et al.* 2011b) and ethylene treatment of apple fruits (Zheng *et al.* 2013).

Hu *et al.* (2015) determined salt tolerance of transgenic apple plants overexpressing MdSOS2L1, a calcineurin B-like protein-interacting proteinkinase. The proteome analysis revealed that enzymes involved in reactive oxygen species (ROS) scavenging, procyanidin biosynthesis and malate metabolism were higher in the MdSOS2L1-overexpressing apple. Other proteomics of rosaceae fruit trees focused on response to pathogens (Clemente-Moreno *et al.* 2013, Li *et al.* 2014, Zhang *et al.* 2015a), Fe deficiency and resupply (Rodríguez-Celma *et al.* 2013), fruit bagging (Feng *et al.* 2011), drought stress (Zhou *et al.* 2015) and early-maturing bud mutant (Liu *et al.* 2014) (**Supplemental Table 1**).

Metabolomics

Metabolomics is the comprehensive study of metabolites in an organism, organ, tissue or cell. Wide variety metabolites, whose molecular size, structures and characters are quite different and unique, are present in organisms. Therefore, different analytical apparatuses are applied on metabolomics. Gas chromatography (GC)-MS is one of the most powerful and widely used methods in metabolomics, because chromatographic resolution of GC is very high. Only volatile compounds can be analyzed in GC-MS, therefore derivatization step to volatilize non-volatile compounds is needed before analysis of non-volatile compounds. Liquid chromatography (LC)-MS, which requires no derivatization steps, is the often used method in metabolomics. Capillary electrophoresis (CE)-MS is another popular method in metabolomics. Generally CE has higher separation efficiency than LC, so CE is suitable for separating wider range of metabolites. However, because CE uses electrophoretic technique, CE-MS can analyze only charged compounds excluding neutral compound. In metabolomics, nuclear magnetic resonance (NMR) has been used to detect compounds including H or C atoms. Compared with MS-based techniques, NMR has a wide range of detection of target compounds, although the detection limit and sensitivity are low.

Metabolome analysis does not need genome sequence data or EST data, but needs standard chemical compounds of metabolites or their MS spectrum data. Most organisms use common primary metabolic pathway. Thus primary metabolites can be easily identified in metabolome analysis because standard chemical compounds of primary metabolites or their MS spectrum data are available. On the other hand, each plant species has unique secondary metabolic pathways. Most of plant secondary metabolic pathways are unclear and standard chemical compounds and MS spectrums of most plant secondary metabolites are unavailable. Therefore, in metabolome analysis, most secondary metabolites are detected as unknown metabolite peaks and cannot be identified. Publications on metabolomics of fruit trees are lesser than transcriptomics or proteomics.

Citrus

Metabolomics and transcriptomics have been performed in ponkan fruit growth (Lin *et al.* 2015) and in postharvest storage of pumelo fruit (Sun *et al.* 2013). In the former study, sugar accumulation and organic acid degradation according to changes in metabolic enzymes were observed in fruit maturation. In the latter study, increase in succinic acid, γ-aminobutyric acid (GABA) and glutamine and decrease in oxoglutaric acid were observed. Interestingly, both studies suggested the involvement of GABA shunt in organic acid degradation in the fruits. One of the physiological disorders of citrus fruit is "puffing", i.e. breakdown of albedo (white part under the peel) and separation between pulp and flavedo (outer colored part of the peel). To elucidate the mechanism of puffing, transcriptome and metabolome analyses ware performed (Ibáñez *et al.* 2014). The multi-omics revealed several alternations of primary metabolism, less citric acid content and down-regulation of GA and cytokinin signaling in puffed fruits. Ballester *et al.* (2013) determined metabolic profiles of albedo and flavedo in elicited navel orange fruits. The results suggested that phenylpropanoids and their derivatives play an important role in the induction of resistance against *Penicillium* spp., which are the major postharvest pathogens of citrus fruit (Ballester *et al.* 2013). Metabolomes of different citrus species and cultivars whose sensitivities against HLB disease are different, were compared. Higher levels of the amino acids, organic acids and galactose in leaves were characteristic of the most sensitive sweet orange varieties (Cevallos-Cevallos *et al.* 2012). On the other hand, differences in the concentration of phenylalanine, histidine, limonin and synephrine in asymptomatic fruits and symptomatic fruits were observed (Chin *et al.* 2014). As Chin *et al.* (2014) suggested, metabolomics has a potential to generate metabolite-based "biomarkers" of important traits of crops, such as HLB resistance in citrus.

Grapevine

Comparing with other fruit trees, much larger number of metabolomics studies has been reported for grapevine.

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Primarily metabolites, including sugars, organic acids and secondary metabolites, such as anthocyanins, proanthocyanidins and resveratrol, are targets of grapevine metabolomics. Some metabolomics focused on volatile compounds which often relate to flavor (Arbulu *et al.* 2013). Many studies compared metabolomes among different grapevine cultivars (Degu *et al.* 2014, Gika *et al.* 2012, Teixeira *et al.* 2014), biotypes (Mulas *et al.* 2011) and wild species (Narduzzi *et al.* 2015). Degu *et al.* (2014) compared metabolomes and transcriptomes of two grapevine varieties, i.e. Cabernet Sauvignon and Shiraz. Da Silva *et al.* (2013) found 1,873 unique genes in the high polyphenol content grapevine cultivar 'Tannat', which are not found in the reference genome of grapevine 'Pinot Noir PN40024'. This study indicates that the reference genome lacks many genes which may relate to varietal phenotypes. Omics-study can reveal differences among cultivars and the information could be useful for crop breeding.

Another major target of metabolomics of grapevine is fruit development. Several studies have compared grapevine metabolomes of before and after véraison showing dramatic shifts of primary and secondary metabolisms after véraison (Dai *et al.* 2013, Fortes *et al.* 2011, Suzuki *et al.* 2015a). Suzuki *et al.* (2015a) showed that anthocyanin was the most abundant phenolic compounds in grape berry skin at harvest, whereas the amount of catechin was higher before véraison. In addition, using MS/MS fragment spectra database to search for the stage specific unidentified metabolites, arginine was identified as a ripening stage specific one. As mentioned above, secondary metabolisms such as anthocyanin synthetic pathways, are induced by berry maturation as well as environmental stresses. Suzuki *et al.* (2015b) reported on metabolomics and transcriptomics and demonstrated clear and specific induction of resveratrol synthetic pathway by ultraviolet (UV) irradiation. The authors showed this induction using the metabolic pathway map, in which metabolome data and transcriptome data were projected by using drafting tool of metabolic pathway map (see the chapter "Omics Databases and Tools"). Metabolomics of grapevine on response to pathogen (Agudelo-Romero *et al.* 2015), insect (Lawo *et al.* 2011), drought stress (Griesser *et al.* 2015) or elevated temperature (Sweetman *et al.* 2014), different *terroir* (Anesi *et al.* 2015, Teixeira *et al.* 2014), polyamine biosynthesis (Agudelo-Romero *et al.* 2014), grape berry and its wine product differences (Aura *et al.* 2013) and antioxidant and antiproliferative properties (Pacifico *et al.* 2011) have been also reported (**Supplemental Table 1**).

Rosaceae fruit trees

Freeze-drying (FD) is often used for sample preparation to remove water from plant tissues before metabolome analysis. Oikawa *et al.* (2011) have checked effect of FD using flesh tissue of European pear fruit. The results showed that FD causes significant decrease of some metabolites, such as succinate and choline. Therefore we FD process should be skipped, if the target metabolites will be degraded. For profiling metabolites of apples, Risticevic *et al.* (2012) have developed and optimized sample preparation procedure for GC-MS, i.e. solid phase microextraction (SPME). Lombardo *et al.* (2011) determined changes in metabolomes during peach fruit development and showed high levels of bioactive polyphenols in early developmental stages. The authors suggested that the high levels of bioactive polyphenols are used as substrates for phenylpropanoid and lignin synthesis of hardening of stone (seed coat). Oikawa *et al.* (2015) reported changes in metabolomes of European pear fruits throughout development and the data is released from "Fruits Omics Database" (**Fig. 2**). The authors quantified over 250 metabolites in pear fruits. Interestingly, changes in each amino acid during fruit development showed completely different pattern. That is, the levels of histidine and phenylalanine were high at bloom stage and then decreased dramatically. Methionine was highest in the middle stage. Proline was highest before boom, decreased at bloom stage and then increased again at ripening stage. Although the meaning of the different fluctuation patterns of amino acids is unclear, they give interesting features of pear fruit development. Tsukaya *et al.* (2015) compared metabolomes of diploid and tetraploid *Arabidopsis thaliana* and diploid and tetraploid fruits of European pear. The authors concluded that metabolite content is not universal nor the direct target of polyploidy-dependent changes. Several metabolomics studies focused on flavor and volatile compounds of fruits. Aprea *et al.* (2011) developed SPME for volatile compounds. They then determined volatile compounds in four different apple varieties and succeeded to identify characteristic markers for each variety. Sánchez *et al.* (2012, 2014) profiled volatile compounds in peach fruits. The authors called their volatile compound analysis "volatilome". Their volatilome of F_1 segregating population and quantity trait locus (QTL) analysis revealed loci controlling the aroma of peach. Sánchez *et al.* (2012) identified 110 volatile compounds and quantified. Combination of hierarchical cluster analysis and metabolomic correlation network analysis revealed not only previously known cluster of peach fruit volatiles but also novel one. Leisso *et al.* (2013) and Lauxmann *et al.* (2014) performed metabolomics of post-harvest storage apple fruits and peach fruits, respectively. The former study determined metabolomes under antioxidant treatment, temperature shifts and peel necrosis. The latter study focused on heat and cold responses.

Other omics studies

Hormonomics is a part of metabolomics. Generally concentrations of plant hormones are very low in all metabolites. Most plant hormones cannot be identified in normal metabolome analysis therefore specialized MS detection system is needed to analyze them. Hormonomics is rarely utilized in fruit tree research and also in general plant science. Only Oikawa *et al.* (2015) have reported comprehensive plant

hormone analysis on fruit trees. Oikawa *et al.* (2015) determined fluctuations of 15 plant hormones, i.e. salicylic acid, JA, JA isoleucine conjugate, ABA, GA1, GA4, indole acetic acid, brassinolide (BL), castasterone (CS), trans-zeatin, dihydrozeatin, isopentenyladenine, trans-zeatin riboside, dihydrozeatin riboside and isopentenyladenine riboside in the fruit development of European pear using LC-tripleQ MS. The obtained hormonome data are available in "Fruits Omics Database" (**Fig. 2**). Concentrations of all plant hormones were very high in the youngest fruit and then decreased dramatically. Only concentrations of ABA, BL and CS increased in the ripening stage. Although increase of ethylene and ABA in fruit ripening stage is often observed, that of BL or CS has almost not been previously reported. BRs, including BL and CS, might be related to fruit ripening at least in European pear. Plant hormones control numerous events in plants, including fruit development. Further hormonomics will elucidate unknown functions of plant hormones in fruit tree growth and fruit development.

Ionomics is the comprehensive study of inorganic ions in an organism, organ, tissue or cell. Ionomics studies is also rare in fruit tree research field. Presently, a few ionomics studies of fruit trees have been reported (Parent *et al.* 2013a, 2013b). Reuscher *et al.* (2014) reported ionome analysis throughout fruit development of European pear and the data is released from "Fruits Omics Database" (**Fig. 2**). The authors tried to detect 27 elements, i.e. Ag, Al, B, Ba, Be, Ca, Cd, Co, Cr, Cu, Fe, Ga, In, K, Mg, Mn, Mo, Na, Ni, P, Pb, Rb, S, Sr, Tl, V and Zn in European pear fruits and its giant mutant fruits (Isuzugawa *et al.* 2014, Nashima *et al.* 2013b, 2014) using an inductively coupled plasmaatomic emission spectrometry (ICP-AES). Among them, 12 elements, i.e. Ca, K, Mg, P, S, B, Cu, Fe, Mn, Mo, Na and Zn, were detected and quantified in pear fruits. Concentrations of all these elements were high especially in the youngest fruit and decrease dramatically, although the decreasing rates were different among elements. Decreasing rates of B, K and Na were slower than other elements. In comparison between European pear fruits and its giant mutant fruits, concentrations of B and Ca in the giant mutant fruits were lower. This might be a cause of the corky spots in the giant mutant fruit as observed by Isuzugawa *et al.* (2014). Seventeen elements, i.e. B, C, Cl, Ca, Cu, Fe, H, K, Mg, Mn, Mo, N, Ni, O, P, S, and Zn are necessary for plant growth and excess amount of some elements, such as Al, Cd and Na, has harmful effect on plants and human also. Therefore ionomics is one of the important techniques to monitor plant health as well as food safety for human.

Omics databases and tools

Useful web pages for fruit omics study are listed in **Table 1**. These web sites provide genome data, microarray raw data, RNAseq raw data, gene expression data, MS spectrum dada, metabolite information, omics data, coexpression analytical tool, metabolic pathway map and its drafting tool and so on. However, presently, most web pages provide limited information support for some plant species.

Genome databases are provided for citrus (Citrus Genome Database), for grapevine (Grape Genome Database, Grape Genome Browser) and for rosaceae plants (Genome Database for Rosaceae; GDR). Plant GDB stores genome data of various plants, including grapevine, peach and papaya. These databases provide information about genome sequence and CDS.

Gene Expression Omnibus (GEO) and Sequence Read Archive (SRA) in National Center for Biotechnology Information (NCBI) store microarray and RNAseq raw data of all organisms, respectively. eFP Browser provides gene expression data and its analytical tool. On demand, eFP Browser displays gene expression patterns in different tissues and organs or induction of gene by different stimuli. Presently, only grape eFP Browser is available for fruit trees. ATTED-II and Co-expression biological Processes (CoP) provide co-regulated gene relationships. Functions of unknown genes could be estimated from gene relationships shown by ATTED-II or CoP. They provide only the systems for grapevine among fruit trees.

MassBank and ReSpect store mass spectrums of chemical compounds. The mass spectrum data is used to estimate metabolites in metabolome analysis. KNApSAcK is the database for various natural chemical compounds and it provides information on metabolites such as molecular weight, structural formula, detected organisms and related articles. Kyoto Encyclopedia of Genes and Genomes (KEGG) is a general database of biological information for all organisms at molecular level derived from omics studies. KEGG PATHWAY Database harbors various metabolic pathway maps. For certain organisms, metabolic pathway maps, in which related proteins, including metabolic enzymes, and their genes are integrated, are provided. For fruit trees, KEGG supports only grapevine metabolic pathway map as a species specified one. Plant Metabolic Network/Plant Metabolic Pathway Database (PMN/PlantCyc) provides metabolic pathway map with enzyme and gene information of various plants, including grapevine and papaya. VitisCyc provides similar metabolic pathway map of grapevine. KaPPA-View 4 KEGG is a drafting tool of metabolic pathway map. Using KaPPA-View 4 KEGG, transcriptome data, proteome data and metabolome data can be projected on a metabolic pathway map easily. KaPPA-View 4 KEGG supports only grapevine among fruit trees. Recently, we have updated the KaPPA-View 4 KEGG system of grapevine to adapt to newer genome data, called V1 (Suzuki *et al.* 2015b). Using the updated system, Suzuki *et al.* (2015b) clearly showed the specific induction of resveratrol synthetic pathway in grape berry skin by UV irradiation. This work shows that metabolic pathway map with omics data can reveal interesting metabolic changes in fruit trees.

Fruits Omics Database is a unique database collecting omics data of fruit trees (**Fig. 2**). Presently, Fruits Omics Database provides transcriptome data (Nashima *et al.*

2013a), metabolome data (Oikawa *et al.* 2015), hormonome data (Oikawa *et al.* 2015) and ionome data (Reuscher *et al.* 2014) of European pear fruits throughout its developmental stages. Proteome data of European pears (Reuscher *et al.* 2016) is scheduled to be released in the database.

All these five omics data, i.e. the transcriptome, proteome, metabolome, hormonome and ionome data of European pear fruits, are derived from the same material, thus all the data are comparable each other. This must be the widest multi-omics study using the same material in plant science field. Fruits Omics Database will collect omics data of other fruit trees.

Conclusion

As shown in the many examples introduced in this article, omics is a powerful approach to identify key genes for important traits, to clarify mechanisms of physiological events and to reveal unknown metabolic pathways in fruit trees. **Supplemental Table 1** is the list of publications on omics studies of citrus, grapevine and rosaceae fruit trees in the last 5 years. Fruit tree researchers have recognized effectiveness of omics and it is becoming more popular in fruit tree research. However the study is still limited to specific crops, such as citrus, grapevine and rosaceae fruit trees. One of the reasons is lack of fundamental information for omics study, such as genome sequence data, EST and chemical compound information.

As described above, analytical costs of NGS is decreasing dramatically. On the other hand, volume of information from NGS and efficiency and accuracy of bioinformatics are increasing and increasing. Due to these situations, genome sequence data and EST for even minor fruit trees will be provided in the near future. This will accelerate the use of transriptomic and proteomic approaches in fruit tree research. Microarray was an indispensable tool for transcriptomics studies before. However RNAseq has become an alternative approach recently. High-throughputs and accurate *de novo* assemble technology of more than 10 million sequence reads from NGS has made it possible to perform transcriptomics without genome or EST data. This technology can be applied in fruit trees transcriptomics studies where limited genome sequence or EST data is available.

The bottleneck of metabolomics is lack of standard chemical compounds and their MS spectrum data on metabolites. In MS analysis of plant extract, several thousands of metabolite peaks are detected but a few hundreds of primary metabolites are identifiable (Oikawa *et al.* 2015). For secondary metabolites, less than a dozen can be identified (Suzuki *et al.* 2015a, 2015b), because of no existence of standard chemical compounds or their MS spectrum dada. Secondary metabolites often contribute to unique fruit characters, such as taste, flavor, color and functionality. Each plant species has unique secondary metabolic pathway and accumulation. High-throughput technologies are needed to identify and clarify synthetic pathways of secondary metabolites so as to accelerate metabolomics studies in plants.

In the research field of fruit trees, enormous undiscovered treasures, i.e. important genes, metabolites, metabolic pathways and unknown physiological processes, lie under the ground. Treasure hunting using omics technology has been just started.

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