



**IN HIGHER PLANTS AS AN EXAMPLE, ONE CAN SEE THAT THE ERA
OF SEQUENCING OF THEIR DIPLOID GENOMES IS COMING**

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Resume

The first complete genome of the plant *Arabidopsis thaliana* was sequenced a quarter of a century ago, but it took another decade and a half to get it reassembled as a diploid genome in the form of haplotypes. Since then by the end of 2024, functionalized diploid genomes with phased assembly have been sequenced for 258 samples representing 143 species of higher plants belonging to 95 genera from 50 families, and the results have been published in 198 articles. Diploid genomes have been sequenced for species of different ploidy, among which most species are diploids, but there are also triploids, tetraploids, hexaploids, several octaploids, and even nonaploids. Already 30 diploid genomes of different plant species have been assembled at the T2T gapless level. For 7 plant species, the diploid genomes are already supplemented by pangenomes, and for two genera, by a super-pangenome. A noticeable increase in the number of genomes with phased assembly of plant haplotypes occurred in the last couple of years, explained by the improvement of DNA sequencing technologies of new generations and by awareness of the need for such information. Interest in phased genome assembly can be attributed to the fact that currently sequenced genomes are essentially quasi-genomes in which fragments of maternal and paternal genomes are interspersed in a mosaic manner, which makes it difficult to identify genotype–phenotype relationships. In most articles describing the phased assembly of haplotyped genomes, it is emphasized that knowledge of nucleotide sequences of a complete set of chromosomes facilitates determination of biosynthesis pathways of various secondary metabolites and the understanding of mechanisms of heterosis manifestation, allows to improve resistance to various pathogens and adaptability to adverse environmental factors, and helps to determine sex in dioecious plants, to develop advanced breeding programs, and to identify processes that took place during domestication. It can be confidently stated that the genomics of higher organisms and plants in particular has entered the era of sequencing of diploid genomes, despite much greater difficulties with obtaining valid results. At the same time, more than 5,000 plant quasi-genomes are already known for approximately 2 thousand species; however, such quasi-genomes, devoid of phased assembly and consisting of mosaic fragments of parental chromosomes, serve only as a necessary stage of analysis in those species whose genomes have not yet been sequenced in order to subsequently assemble haplotypes in a phased manner by means of chromosomes at the T2T gapless level. The latter is a higher level of establishing the structure of genomes and of their annotation.

Keywords: sequencing, genome, reference genome, quasi-genome, pangenome, super-pangenome, T2T genome, diploid genome, phased genome, haplotype-resolved genome, haplotypes, genome assembly

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Introduction

On the centenary of the term "genome," we have already stated that sequencing of quasi-genomes with mosaic assembly of a haploid set of chromosomes must stay in the past [1]. It may be recalled that the term "nuclear genome" now refers to the entire set of DNA sequences from a haploid set of chromosomes. Therefore, each higher organism (with some exceptions), and plants in particular, actually contains two different genomes¹ in the nucleus, inherited from its parental forms, and even plants that now reproduce mainly vegetatively have arisen at some point through one or another crossing. Moreover, polyploid forms characteristic of many species should be regarded as having undergone functional diploidization after polyploidization and as consisting of sets of subgenomes. If the sets of subgenomes are the same, then it is an autopolyploid, and if they are of different quality, then it is an allopolyploid. Moreover, H. Winkler, back in 1920, proposed using the new word "genome" for a haploid set of chromosomes as the material basis of an organism's species and noted that if a genome contains more than one such unit, then it should be called homogenomatic, and if different units, then heterogenomatic; this thinking was much ahead of its time, foreseeing the existence of subgenomes [2].

Growing interest in the sequencing of such diploid genomes² of higher organisms and plants in particular is easily explained by the fact that only knowledge of nucleotide sequences of a complete set of chromosomes (in the case of species with diploid status, rather than gametophytes) allows researchers to identify a genotype–phenotype relationship, whereas quasi-genomes with a mosaic assembly of determined sequences from a half set of chromosomes do not permit to fully to assess their real contribution to a structural and functional state. Previous DNA sequencing methods, including those of new first generations, made it possible to determine nucleotide sequences of complete diploid genomes only with great difficulty. On the other hand, with the development of sequencing technologies, including monomolecular sequencing, it became possible to obtain long and ultra-long reads and to implement a phased haplotyped assembly of two plant nuclear genomes. This process has begun and with noticeable acceleration, as will become apparent below.

The history of the development of DNA sequencing methods at the end of the 20th century and the

evolution of new-generation DNA-sequencing techniques at the beginning of the 21st century have been discussed in detail in other publications [3-4], and we will not touch on this topic here. At the same time, due to high-throughput sequencing, the number of haplotype-resolved genomes with phased assembly has grown substantially in recent years, and there is a need to summarize the currently available information on such diploid genomes, which is what this article is about. First of all, it is worth recalling existing levels of assembly of higher organisms' genomes.

Assemblies of quasi-genomes of higher organisms

Currently, most genome-sequencing projects read DNA nucleotide sequences from a complete set of chromosomes, and as a result, only half of them are assembled, with fragments of the maternal (M) and paternal (P) genomes arranged in a random mosaic order. That is, during the sequencing of total DNA, multiple fragments of the M genome are sequenced in an interspersed form as m_n and the P genome as p_n , and instead of two true genomes, i.e., ... mmmmmmmmmmm ... and ... pppppppppppp ..., their assembly is performed as a quasi-genome: ... mppmmpmmpmmp ...; this is far from the true distribution of such fragments on maternal and paternal chromosomes, in other words, from the true distribution by haplotypes. And such an assembly can lead to a distorted reconstruction of amino acid sequences of proteins, with resulting undesirable consequences for predictions of their functioning. Thus, if we sequence some plant genome with a size of 1 billion bp, in actuality we are sequencing two its nuclear genomes with a total size of 2 billion bp, but usually, one quasi-genome with a size of 1 billion bp is assembled.

That is, in this case, for this quasi-genome $1 + 1 \neq 2$, but $1 + 1 = 1$. In other words, in fact, half of the genetic information is lost, some of which may be critical. At the same time, with whole-genome sequencing, it is customary to achieve a certain coverage per genome, for example, a multiple of 30, but for two nuclear genomes with inevitably different sequences from the full set of chromosomes, the coverage actually turns out to be only 15-fold, which, according to probability theory, is not enough to confidently read all fragments of two nuclear genomes of one higher organism by modern techniques. Nevertheless, such sequencing is still being performed, and it is even necessary (for now) for those species whose genomes are unknown because the quasi-genome reconstructed in this way, acting as a reference at this stage, serves as a further guideline for better assemblies of both quasi-genomes and a step toward sequencing of their two haplotypes as independent genomes.

When DNA is sequenced, many reads are formed, representing raw data, and as a consequence of

¹ according to the current definition of the genome.

² It should be noted that some confusion sometimes arises in conjunction with sequencing of diploid genomes as haplotypes with phased assembly; this is because a number of articles describe the sequencing of "diploid genomes," but they refer to the usual quasi-genomes of "diploid species" of organisms.

computer processing and assembly, they turn into elongated contigs and scaffolds, compilations of which make up a certain genome. Nevertheless, they may not cover the entire genome, but if it is being sequenced for the first time, then this level (still) gives an impression of a "complete" reading of this genome, called a "draft." It should be noted here that if the genome of a certain species is being sequenced for the first time, then there can be no other assembly besides *de novo*. Resequencing of an already known the (quasi)genome of other similar samples poses another problem. In this case, researchers make claims about resequencing and assembly of raw data based on a known reference sequence.

Chromosomal representation of data should be considered the next level of sequencing/assembly of complete genomes, and of course, carries more important information. At the same time, nucleotide sequences in them are still quasi-haploid. In the literature, one can find different designations of such genomes: chromosomal-level or chromosome-scale or pseudochromosomes or pseudomolecules.

Bringing sequencing results to the "telomere-to-telomere" level, also known as "T2T," is actually a more accurate and complete version of a chromosome level assembly. Many articles have already emphasized that plant genomes are assembled at a T2T, gap-free, or gapless level, but they also remain quasi-genomes. The assembly of such T2T quasi-genomes has started relatively recently and has caused a significant increase in interest in this type of genomic data representation, but we will not discuss them here because there is another article on this topic in this issue of journal [5].

As information about quasi-genomes of identical species of organisms, including plants, has accumulated, it has become clear that their polymorphism is extremely high and that it is impossible to work with a single reference genomic sequence for one species. Thus, the concept of a "pangenome" has appeared, reflecting already diverse variations in nucleotide sequences of genomes from individual representatives of a species/genus, from various plant varieties in particular. Nonetheless, plant pangenomes have also necessitated a separate article [6].

Diploid genomes with phased haplotyped assembly

It is extremely important to sequence complete diploid genomes of organisms (or genomes with haplotyped assembly or phased ones); these genomes carry information about both allelic variants of genes from paired chromosomes or their hemizygous state; for this reason, such genomes are no longer quasi-haploid. Moreover, the assembly of such diploid genomes is carried out exclusively in the *de novo* format because it is

important to find differing regions, and in particular indels (insertion/deletions), which are more likely to be missed during the assembling according to the reference genome, which serves only as a kind of guideline in this case. It is even easier to overlook an allelic imbalance as PAV genes (presence/absence variations of genes) and CNVs (copy number variations) and accordingly to underestimate their contribution to the functional state of the plant in question, given that it is PAVs and CNVs that make the greatest contribution to a difference between plants of the same species (varieties are different from each other). Meanwhile, such sequencing involves much more effort and, in addition to greatly increased coverage, requires the use of long and ultra-long reads, Hi-C seq, Strand-seq, optical mapping of genomes, and other approaches, for example, trio sequencing, when possible.

Despite the difficulties with such diploid sequencing, interest in it is growing, as evidenced by the number of published articles, increasing each year. The number of plant species/genera for which diploid genomes have been identified is growing too. In total, more than 3500 complete plant genomes have been sequenced for one and a half thousand species as of autumn 2023, as one can see in the 3N database <http://ibi.zju.edu.cn/N3database/index.php> [7]. Unfortunately, in this database and another similar one https://www.plabipd.de/pubplant_main.html, diploid plant genomes are not separated from others; however, it seems that soon we will have to pay special attention to sequenced plant genomes with phased assembly of haplotypes.

The information currently available here is summarized in a table in which haplotype designations used by authors of the original articles are used. As for assembly levels of such diploid genomes, they are also given as indicated by those authors. Each sequence of diploid genomes in this table is presented according to a two-level principle: a year of publication of articles and scientific names of plants in alphabetical order. It should be noted that starting from 2023, 28 diploid genomes have already been assembled at the T2T level, and nine diploid genomes have been supplemented with pangenomes of various species, including one super-pangenome of a genus, as highlighted in the table in lilac and yellow colors, respectively. To compile phased genomes, a number of researchers have employed approaches involving trio sequencing or gamete sequencing, which are highlighted in green and azure colors, respectively, in the table.

Another article on advancements in plant genome assembly contains information on diploid genomes of slightly more than 30 plant species but is focused on sequencing and assembly strategies [8].

Table 1

Species	Common name, cv.	Ploidy	The size of the entire set of chromosomes or phased genomes (haplotypes) (Mb)	Assembly	Reference
2016					
<i>Arabidopsis thaliana</i>	Thale cress	2n=2x=10	two haplotigs, 105 each	Trio-binning	9
<i>Vitis vinifera</i>	Grape, 'Cabernet Sauvignon'	2n=2x=38	two haplotigs, 368 each		
2017					
<i>Ipomoea batatas</i>	Sweet potato, 'Taizhong6'	2n=6x=90	∑ - 870	15 Pseudochromosomes	10
2018					
<i>Capsicum annuum</i>	Pepper	2n=2x=24	pseudohap1 and pseudohap2 - 3210 for each	Pseudomolecules	11
<i>Oryza longistaminata</i>	African wild rice	2n=2x=24	Hap1 - 350; Alternative contigs - 258	Haplotigs	12
<i>Saccharum spontaneum</i>	Sugarcane, 'AP85-441'	2n=4x=32	∑ (A, B, C, D) - 2 × 2900	Pseudo-chromosomes	13
2019					
<i>Cerasus x yedoensis</i>	Cherry 'Somei-Yoshino'	2n=2x=16	CYEspachiana_r3.1 - 350; CYEspacioza_r3.1 - 339		14
<i>Manihot esculenta</i>	Cassava, '60444'; 'TME3'	2n=2x=36	∑ - 1277; ∑ - 1225	Pseudochromosomes	15
<i>Pyrus bretschneideri</i>	Pear	2n=2x=34	Haplotype A - 546; Haplotype B - 538	Gamete-based	16
<i>Vitis vinifera</i>	Grape, 'Carmenere'	2n=2x=38	∑ - 1040		17
<i>Vitis vinifera</i>	Grape, 'Zinfandel'	2n=2x=38	2 × 306	Haplotigs	18
<i>Vaccinium corymbosum</i>	Blueberry	2n=4x=48	∑ - 1679	Chromosome-level pseudomolecules	19
2020					
<i>Amaranthus tuberculatus</i> × <i>A. hybridus</i>	Amaranth hybrid	2n=2x=16	∑ - 675; 503 (haploid genomes)	Partial	20
<i>Ficus carica</i>	Fig, 'Dottato', female	2n=2x=26	∑ - 333 (haploid - 13 pseudomolecules)	Haplotigs	21
<i>Malus domestica</i>	Apple, 'Gala'	2n=2x=34	Haplome A - 657; Haplome B - 577	Super pangenome	22
<i>Medicago sativa</i>	Alfalfa	2n=4x=32	hap1 - 679; hap2 - 700; hap3 - 682; hap4 - 676	Chromosome-level	23
<i>Prunus armeniaca</i>	Apricot 'Rojo Passion'	2n=2x=16	'Currot' haplotype - 216; 'Orange Red' haplotype - 215	Chromosome-level, gamete-binning	24
<i>Prunus avium</i>	Sweet cherry, 'Tieton'	2n=2x=16	∑ - 2 × 344	Chromosome-scale	25
<i>Solanum tuberosum</i>	Diploid potato	2n=2x=24	∑ - 1670	Pseudochromosomes	26
<i>Vanilla planifolia</i>	'Daphna'	2n=2x=28	Haplotype A - 736; Haplotype B - 744	Chromosome-scale	27
<i>Vitis riparia</i> × <i>V. cinerea</i>	Hybrid grape 'Bömer'	2n=2x=38	Two haplophases - 618 each	Partially phased	28
<i>Vitis vinifera</i>	Grape, 'Cabernet Sauvignon'	2n=2x=38	hap1 - 449; hap2 - 444		29

Table 1, cont.

		2021		
<i>Ananas comosus</i>	Pineapple 'MD2'	2n=2x=50	P0 – 543; P1 – 531	Phased chromosomes 30
<i>Camellia sinensis</i>	Tea	2n=2x=30	HA – 2920; HB – 2950	Chromosomal-level 31
<i>Camellia sinensis</i>	Tea	2n=2x=30	Haplotype A – 3060; Haplotype B – 2920	Chromosomal-level 32
<i>Camellia sinensis</i>	Tea, 'Fudingdabai'	2n=2x=30	Σ - 2 × 3110	Gamete-based 33
<i>Carya illinoensis</i>	Pecan, 'Pawnee'	2n=2x=32	Primary assembly – 674; Alternative haplotype - 603	Chromosome-scale, pangenome 34
<i>Cerasus × kanzakura</i>	Hybrid cherry, 'Kawazu-zakura'	2n=2x=16	<i>C.campanulita</i> haplotype – 267; <i>C.specioza</i> haplotype – 242	Pseudomolecule 35
<i>Cerasus × kanzakura</i>	Hybrid cherry, 'Atami-zakura'	2n=2x=16	<i>C.campanulita</i> haplotype – 262; <i>C.specioza</i> haplotype – 257	sequences 35
<i>Chenopodium quinoa</i>	Quinoa, 'CHEN125'	2n=4x=36	Σ - 1320 (genome)	Hapotype information 36
<i>Fragaria × ananasa</i>	Strawberry, Royal Royce	2n=8x=56	Phase-1 – 784; Phase-2 - 784	Pseudomolecules, trio-binning 37
<i>Humulus lupulus</i>	Hop	2n=2x=20	Σ - 2 × 2,800	38
<i>Hydrangea macrophylla</i>	Hydrangea	2n=2x=18	Phase 0 – 2256; Phase 1 – 2227	Pseudomolecules 39
<i>Mangifera indica</i>	Mango, 'Tommy Atkins'	2n=2x=40	Σ - 439 (haploid)	Pseudomolecules 40
<i>Manihot esculenta</i>	Cassava	2n=2x=36	Primary – 720; Alternate - 720	41
<i>Muscadinia rotundifolia</i>	Grape, 'Trayshed'	2n=2x=20	Haplotype 1 – 400; Haplotype 2 – 369; Unplaced - 62	Chromosome-scale 42
<i>Vaccinium myrtillus</i>	Bilberry	2n=2x=24	Σ - 464 (haploid)	Haplotype-like contig set 43
<i>Zingiber officinale</i>	Ginger, Zhangliang	2n=2x=22	haplotype genome A – 1624; haplotype genome B – 1424	Pseudochromosomes 44
<i>Zingiber officinale</i>	Ginger	2n=2x=22	Haplotype 1 – 1524; Haplotype 0 – 1504	Chromosome-scale 45
		2022		
<i>Ananas comosus</i>	Pineapple 'Yugafu'	2n=2x=50	Haplotype 1 – 550; Haplotype 2 - 542	Trio-binning 46
<i>Artemisia annua</i>	Mugwort, LQ-9	2n=2x=18	haplotype0 – 1549; haplotype1 – 1474	Chromosome-level 47
	Mugwort, HAN1	2n=2x=18	haplotype0 – 1590; haplotype1 – 1383	
<i>Asparagus kiusiamus</i>	Asparagus, male	2n=2x=20	AKIK1p1 – 1630; AKIK1p2 – 1629	Chromosome scale 48
	Asparagus, female	2n=2x=20	AKIK2p1 – 1580; AKIK2p2 – 1579	
<i>Bidens hawaiiensis</i>	Kookoolau	2n=6x=72	Asm1 – 2748; Asm2 – 2756	49
<i>Bletilla striata</i>	Baiji	2n=2x=32	Haplotype A – 2368; Haplotype B – 2431	Chromosome scale pseudomolecules 50
<i>Bupleurum chinense</i>	Chinese thoroughwax	2n=2x=12	Hap0 – 621; Hap1 – 600	Chromosome-Level 51
<i>Cynodon dactylon</i>	Bermuda grass	2n=2x=36	A1 – 236; A2 – 231; B1 – 271; B2 - 266	Pseudo chromosomes 52
<i>Dendrocalamus latiflorus</i>	Bamboo	2n=6x=70	Σ - 2 × 2,737	Chromosome-scale 53
<i>Fragaria × ananasa</i>	Strawberry, 'FL 15.89-25'	2n=8x=56	F12 haplotype – 827; Bea haplotype - 839	Pseudomolecules, trio-binning 54
<i>Litchi chinensis</i>	Lychee, 'Feizixiao'	2n=2x=30	HY – 470; HH - 470	Pseudochromosomes 55
<i>Malus domestica</i>	Apple, 'Honeycrisp'	2n=2x=34	Haplome 1 - 674; Haplome 2 - 660	Chromosome-scale 56

Table 1, cont.

<i>Manihot esculenta</i>	Cassava	2n=2x=36	Haplotype 1 - 762; Haplotype 2 - 706	57
<i>Medicago sativa</i>	Alfalfa, 'Zhongmu-4'	2n=4x=32	hap1 - 695; hap2 - 641; hap3 - 637; hap4 - 588	58
<i>Persea americana</i>	Avocado	2n=2x=24	Σ - 2 × 900	59
<i>Pogostemon cablin</i>	Patchouli	2n=4x=64	Σ - 1940	60
<i>Populus tomentosa</i>	Poplar	2n=2x=38	Σ - 2 × 740	61
<i>Populus × tomentosa</i>	Chinese white poplar	2n=3x=57	Σ - 1580	62
<i>Saccharum spontaneum</i>	Sugarcane, 'Np-X'	2n=4x=40	Σ - 2759	63
	Potato:			
	'Altus'		Σ - 2140	
	'Atlantic'		Σ - 2447	
	'Avenger'		Σ - 2345	
	'Castle Russet'	2n=4x=48	Σ - 2217	64
	'Colomba'		Σ - 1990	
	'Spunta'		Σ - 1992	
<i>Solanum tuberosum</i>	Potato, Cooperation-88	2n=4x=48	C88_H1 - 829; C88_H2 - 788; C88_H3 - 774; C88_H4 - 763	65
<i>Solanum tuberosum</i>	Potato, 'Otava'	2n=4x=48	Σ four haplotypes - 3100	66
<i>Suaeda glauca</i>	Seepweed	2n=2x=18	haplotype 1 - 647; haplotype 2 - 638	67
<i>Trifolium pratense</i>	Red clover	2n=2x=14	Primary haplotype - 419; Alternate haplotype - 353	68
<i>Vaccinium darrowii</i>	Blueberry	2n=2x=24	Primary assembly - 565; Secondary- 471	69
<i>Vanilla planifolia</i>	Vanilla	2n=2x=32	Σ - 3400	70
<i>Vitis labruscana</i> × <i>V. vinifera</i>	Grape, 'Shine Muscat'	2n=2x=38	Phased genome VSMph_r1.0 - 1004	71
	Grape, Rootstock Richter 110		Haplotype <i>V.berlandieri</i> - 495; Haplotype <i>V. rupestris</i> - 423	
<i>Vitis vinifera</i> ssp. <i>vinifera</i>	Grape, Rootstock Kober 5BB	2n=2x=38	Haplotype <i>V.berlandieri</i> - 505; Haplotype <i>V. riparia</i> - 491	72
	Grape, Rootstock 101-14		Haplotype <i>V. riparia</i> - 492; Haplotype <i>V. rupestris</i> - 492	
<i>Vitis vinifera</i>	Grape, 'Nebbiolo'	2n=2x=38	Primary assembly - 560; Alternate haplotype - 533	73
2023				
<i>Actinidia chinensis</i>	Kiwifruit, 'Hongyang'	2n=2x=58	HY4P - 606; HY4A - 599	74
<i>Actinidia chinensis</i>	Kiwifruit, 'Donghong'	2n=2x=58	Σ - 1216	75
<i>Actinidia latifolia</i>	Kiwifruit, 'Kuoye'	2n=2x=58	Σ - 1280	
<i>Actinidia eriantha</i>	Kiwifruit, 'Midao 31'	2n=2x=58	MDHAPA - 619; MDHAPB - 611	76
<i>Antirrhinum hispanicum</i>	Snapdragon, 'AhS ₇ S ₈ '	2n=2x=16	S7 - 502; S8 - 487	77

Table 1, cont.

<i>Capsicum annuum</i>	Hybrid pepper	2n=2x=24	HDA149v1.0 – 3100; HDA330V1.0 – 3118	Trio-binning, pseudomolecules	78
<i>Chaenomeles specioza</i>	Quince	2n=2x=34	Hap1 – 592; Hap2 – 608	T2T	79
<i>Citrus australis</i>	Round lime	2n=2x=18	hap1 – 298; hap2 – 290	Pseudochromosomes	80
<i>Citrus limon</i>	Lemon	2n=2x=18	∑ - 633: Hap 1 - 299; Hap 2- 334	All pair chromosomes	81
<i>Citrus sinensis</i>	Sweet orange, 'Valencia'	2n=2x=18	DVC_A – 299; DVC_B - 299	Chromosome-level	82
<i>Citrus sinensis</i>	Sweet orange, 'Newhall'	2n=2x=18	primary and secondary haplotypes – 618 each	chromosomes	83
<i>Coriaria nepalensis</i>	Masuri berry	2n=4x=40	∑ - 620	Chromosome-scale	84
<i>Cucumis melo</i> ssp. <i>agrestis</i>	Melon var. <i>acidulus</i>	2n=2x=24	Hap1 – 373; Hap2 – 364	T2T	85
<i>Cyclocaria paliurus</i>	Wheel wingnut	2n=2x=32 2n=4x=64	PA-dip – 586; PG-dip - 583 ∑ - PA-Tetra – 2,168	Pseudo-chromosomes	86
<i>Cyclocaria paliurus</i>	Wheel wingnut	2n=2x=32 2n=4x=64	∑ - 1202 ∑ - 2355	Chromosome-level	87
<i>Dianthus caryophyllus</i>	Carnation, 'Aili'	2n=2x=30	hap1 – 584; hap2 – 578	Chromosome-scale	88
<i>Dianthus caryophyllus</i>	Carnation, 'Baltico'	2n=2x=30	Hap1 – 564; Hap2 – 568	T2T	89
<i>Diospyros kaki</i>	Persimmon, 'Xiaoguoqianshi'	2n=6x=90	DkaA – 763; DkaB – 725; DkaC – 685; DkaD – 664; DkaE - 645; DkaF - 581	Chromosome-level pseudomolecules	90
<i>Eucalyptus grandis</i> × <i>E.urophylla</i>	<i>Eucalyptus</i>	2n=2x=22	Haplogenome 1 – 566; Haplogenome 2 - 544	Pseudo-chromosomes	91
<i>Eutrema japonicum</i>	Wasabi, 'Mazuma'	2n=4x=28	∑ - Hap1A, Hap1B, Hap2A, Hap2B – 1512	Chromosomal-level	92
<i>Fagopyrum esculentum</i>	Buckweed	2n=2x=16	∑ - 2 × 1219 ∑ - 2 × 453	Chromosome-level	93
<i>Fagopyrum tataricum</i>	Buckweed	2n=2x=16	Fe-haplotype 1 – 1234; Fe-haplotype 2 – 1193 Ft-haplotype 1 – 453; Ft-haplotype 2 – 446	Chromosome-level	94
<i>Fragaria chiloensis</i>	Strawberry	2n=8x=56	hap 1 - 839; hap 2 - 824	Partially T2T	95
<i>Fragaria virginiana</i>	Strawberry	2n=8x=56	hap 1 - 787; hap 2 - 769	Chromosomes	96
<i>Fragaria</i> × <i>ananasa</i>	Strawberry, 'Yanli'	2n=8x=56	Hap1 – 824; Hap2 - 808	Chromosome-level	97
<i>Humulus lupulus</i>	Hop, 'Cascade'	2n=2x=20	∑ - 2 × 3058	Chromosome-level	97
<i>Hydrangea macrophylla</i>	Hydrangea, 'Endless summer'	2n=2x=18	∑ - 2220	Pseudochromosomes	98
	Hydrangea, 'Veitchii'	2n=2x=18	∑ - 2210	T2T	99
<i>Jasminum sambac</i>	Jasmine	2n=2x=26	HA – 537; HB – 537	Chromosome-scale	100
<i>Malus angustifolia</i>	Apple	2n=2x=34	Haplotype 1 – 413; Haplotype 2 – 412	Chromosome-level	101
<i>Malus x domestica</i>	Apple, 'Antonovka'	2n=2x=34	HAP1 – 651; HAP2 – 636	Chromosome-scale	102
<i>Malus fusca</i>	Crabapple	2n=2x=34	Haplotype 1 – 682; Haplotype 2 – 644	Chromosome-level	102
<i>Manihot esculenta</i>	Cassava	2n=2x=36	hap1 – 693; hap2 – 664	Chromosome-level	103

Table 1, cont.

<i>Manihot esculenta</i>	Cassava, 'Xinxuan 048'	2n=2x=36	hapA – 665; hapB – 664	T2T	104
<i>Melaleuca quinquenervia</i>	Honey plant - paperbark tree	2n=2x=22	Haplotype A – 269; Haplotype B – 271	Chromosome-level, pseudo-phased	105
<i>Microcos paniculata</i>	Buzhaye	2n=2x=18	Haplotype A – 399; Haplotype B – 393	Pseudo-chromosomes	106
<i>Musa acuminata</i>	Banana, 'Baxijiao' (Cavendish)	2n=3x=33	BXJHap1 – 477; BXJHap2 – 477; BXJHap3 – 469	T2T	107
<i>Musa acuminata</i>	Banana	2n=2x=22	MAH1 – 469; MAH2 – 470	T2T	108
<i>Musa acuminata</i>	Banana: 'Platain' 'Silk'	2n=3x=33	Haplotype A1 - 499; Haplotype A2 – 458; Haplotype B – 455 Haplotype A1 - 496; Haplotype A2 – 451; Haplotype B - 486	Pseudochromosomes	109
<i>Nymphoides indica</i>	Marshwort	2n=2x=18	Haplotype A – 571; Haplotype B – 588	Pseudochromosomes	110
<i>Panicum miliaceum</i>	Proso millet	2n=2x=18	subgenome 1 – 470; subgenome 2 - 367	Pseudo-chromosomes	111
<i>Populus tremula</i> × <i>P. alba</i>	Hybrid aspen	2n=4x=38	Pt-HAP1 – 394; Pa-HAP2 – 402	Chromosomal pseudomolecules	112
<i>Quercus glauca</i>	Ring-cup oak	2n=2x=24	haplotype1 – 902; haplotype2 – 913	Chromosome-level	113
<i>Quercus rubra</i>	Red oak	2n=2x=24	Primary assembly – 704; alternate haplotype – 623	Not fully phased	114
<i>Quercus variabilis</i>	Cork oak	2n=2x=24	Haplotype A – 789; Haplotype B - 768	T2T	115
<i>Rheum officinale</i>	Rhubarb	2n=4x=44	Σ - 7682	Chromosome-scale	116
<i>Rhododendron</i> × <i>pulchrum</i>	Rhododendron	2n=4x=52	Haplotype 1 – 509; Haplotype 2 – 496	Chromosome-scale	117
<i>Rhododendron vialii</i>	Rhododendron	2n=4x=52	Haplotype A – 532; Haplotype B – 521	Pseudochromosomes	118
<i>Salix purpurea</i>	Willow, clone 94003	2n=2x=38	Haplotype 1 – 447; Haplotype 2 – 406	Pseudomolecules	119
<i>Suaeda glauca</i>	Seepweed	2n=2x=18	HapA – 518; HapB - 508	Chromosome-Scale	120
<i>Syzgium samarangense</i>	Wax apple	2n=4x=44	Σ - 1590	Chromosome-scale	121
<i>Trifolium repens</i>	White clover	2n=4x=32	Hap1 – 998; Hap2 – 1,009	Chromosome-Level	122
<i>Vaccinium corymbosum</i>	Blueberry, 'W85'	2n=2x=24	Phase 0 - 703; Phase 1 - 643	Chromosome-scale	123
<i>Vitis acerifolia</i>			haplotype 1 - 486; haplotype 2 – 482; unplaced - 55		
<i>Vitis aestivalis</i>			haplotype 1 - 548; haplotype 2 – 545; unplaced – 97		
<i>Vitis arizonica</i>			haplotype 1 - 466; haplotype 2 – 423; unplaced – 66		
<i>Vitis berlandieri</i>			haplotype 1 - 554; haplotype 2 – 549; unplaced - 114		
<i>Vitis girdiana</i>		2n=2x=38	haplotype 1 - 464; haplotype 2 – 476 unplaced – 65	Chromosome scale, super-pangenome	124
<i>Vitis manticola</i>			haplotype 1 - 521; haplotype 2 - 505; unplaced – 99		
<i>Vitis mustangensis</i>			haplotype 1 - 454; haplotype 2 – 432; unplaced – 71		
<i>Vitis riparia</i>			haplotype 1 - 520; haplotype 2 – 506; unplaced – 113		
<i>Vitis</i> × <i>doaniana</i>	Grape, 'PI 588149'	2n=2x=38	Hap1_chr - 486; Hap2_chr - 486		125
<i>Vitis</i> hybrid	Grape, 'Gf:99-03'	2n=2x=38	Gf9921 – 511; Gf9918 - 544	Pseudochromosomes	126
<i>Vitis vinifera</i>	Grape, 'Yan73'	2n=2x=38	Hap1 – 501; Hap2 - 493	T2T	127
<i>Vitis vinifera</i>	Grape, 'Merlot'	2n=2x=38	Haplotype Merlot_CF – 499; Haplotype Merlot_MG - 499	Pseudomolecules, trio-binning	128

		2024		T2T		129
		Hap1_T2T – 504; Hap2_T2T – 496		Hap1 – 602; hap2 – 598		130
<i>Actinidia arguta</i>	Hardy kiwifruit, 'Longcheng No2'	2n=4x=116	hapA – 615; hapB – 595; hapC – 570; hapD – 552	Chromosomes		130
Kiwifruit:						
	'Biyu'		hap1 – 602; hap2 – 598			
	'Hongyang'		hap1 – 606; hap2 – 599			
	'Hort 16A'		hap1 – 602; hap2 – 601			
<i>Actinidia chinensis</i>	'Huangyang'	2n=2x=28	hap1 – 604; hap2 – 601	Chromosome-scale, pangenome		131
	'Jinni'		hap1 – 604; hap2 – 595			
	'Jinpai'		hap1 – 603; hap2 – 592			
	'Zps 18'		hap1 – 602; hap2 – 603			
<i>Amborella trichopoda</i>	Amborella	2n=2x=26	Hap1 – 708; Hap2 – 700			132
<i>Ananas comosus</i> var. <i>microstachys</i>	Pineapple, 'Yu Ling Long'	2n=2x=50				
<i>Ananas comosus</i> var. <i>comosus</i>	Pineapple, 'Ba Li'	2n=2x=50	For all varieties cumulative	T2T, gap-free		133
<i>Ananas comosus</i> var. <i>erectifolius</i>	Pineapple, 'Li Ye'	2n=2x=50	sizes of each types – 423			
<i>Antiaris toxicaria</i>	Upas tree	2n=2x=26	Haplotype A – 682; Haplotype B – 661	Pseudomolecules		134
<i>Bambusa odashimae</i>	Bamboo	105 Chr (Nonaploid)	Hap I – 1240; Hap II – 1060; Hap III – 1030			135
<i>Bidens</i> <i>alba</i>	Bidens	2n=2x=24	∑ - 1874 each			
		2n=4x=48	∑ - 3749 each diploid			
<i>Cosmos bipinnatus</i>	Cosmea	2n=2x=12	∑ - 1015 each	Chromosome-level		136
		2n=2x=32	∑ - 3928 each			
<i>Dahlia pinnata</i>	Dahlia	2n=4x=64	∑ - 7857 each diploid			
<i>Camellia oleifera</i>	Tea oil camellia	2n=4x=60	Haplotype A – 2763; Haplotype B – 2750; Haplotype C – 2759; Haplotype D – 2795	Chromosome-level		137
<i>Castanea sativa</i>	Chestnut, 'Marrone Di Chiusa Pesio'	2n=2x=24	Haplotype 1 – 715; Haplotype 2 – 713	Chromosome-level		138
<i>Chionanthus retusus</i>	Chionanthus, 'Xuezaohua'	2n=2x=46	Two haplotypes – 687 and 683	T2T, gap-free		139
<i>Chrysanthemum indicum</i>	Chrysanthemum	2n=2x=18	Hap A – 3080; Hap B – 3090	Chromosome scale		140
<i>Citrus australasica</i>	Finger lime	2n=2x=18	hap1 – 321; hap2 – 323			141
<i>Citrus australasica</i>	Finger lime		Primary hap 1 – 336; Alternate hap 2 – 335			
<i>Citrus glauca</i>	Desert lime	2n=2x=18	Primary hap 1 – 376; Alternate hap 2 – 379	Chromosomal pseudomolecules		142
<i>Citrus inodora</i>	Australian wild lime		Primary hap 1 – 303; Alternate hap 2 – 299			
<i>Citrus changshanensis</i>	Huyou	2n=2x=18	Hap1 – 323; Hap2 – 311			143
<i>Citrus sinensis</i>	Sweet orange	2n=2x=18	Hap 1 – 320; Hap 2 – 305			144
<i>Coptis teeta</i>	Mishimi Tita	2n=2x=18	Hap 1 – 882; Hap 2 – 859			145
<i>Corylus avellana</i>	Hazelnut, 'Jefferson'	2n=2x=22	Hap1 – 349; Hap2 – 352	Chromosome-level		146

Table 1, cont.

<i>Corydalis yanhusuo</i>	Yuan-hu	2n=4x=32	HapA1 – 61; HapA2 – 60; HapA3 – 60; HapB – 62	Chromosome-scale	147
<i>Dracaena cambodiana</i>	Dragon's blood tree	2n=2x=40	haplotype 1 – 1015; haplotype 2 – 1003	Chromosome-level	148
<i>Eucalyptus regnans</i>	Mountain Ash	2n=2x=22	Hap1 – 523; Hap2 – 504	T2T	149
<i>Ehretia macrophylla</i>	Wild loquat	2n=2x=40	Hap1 – 1,818; Hap2 – 1,580	Chromosome-level	150
<i>Firmiana kwangsiensis</i>	Firmiana	2n=2x=40	Haplotype A – 1169; Haplotype B – 1157	T2T	151
<i>Fleuggea virosa</i>	Bushweed	2n=2x=26	Hap lotype1 – 487; Haplotype 2 – 477	Chromosome-level	152
<i>Fragaria × ananasa</i>	Strawberry, 'Benihoppe'	2n=8x=56	2 Haplotigs – 851, 821	Gap-free	153
<i>Fragaria × ananasa</i>	Strawberry, 'Beni hoppe'	2n=8x=56	Hap1 – 785; Hap2 - 789		154
<i>Fragaria moupinensis</i>	Wild strawberry	2n=4x=28	Σ - 896	T2T	155
<i>Helianthus tuberosus</i>	Jerusalem artichoke	2n=6x=102	Σ - 21600	Pseudochromosomes	156
<i>Hibiscus sabdariffa</i>	Hibiscus	2n=2x=36	Hap 1 – 1420; Hap 2 – 1480		157
<i>Juglans regia</i>	Wild walnut	2n=2x=32	hap1 – 563; hap2 – 561	Pseudochromosomes	158
<i>Ligusticum chuaxiong</i>	Ligusticum	2n=2x=22	HapA – 3431; HapB – 3308	Chromosome-level	159
<i>Malus coronaria</i>	Apple	2n=2x=34	Haplome 1 – 666; Haplome 2 – 675		160
<i>Malus ioensis</i>	Apple	2n=2x=34	Haplome 1 – 644; Haplome 2 – 661		160
<i>Malus domestica</i>	Apple, Red Fuji	2n=2x=34	HapA - 668; HapB – 668	Anchored in chromosomes	161
	Apple, 'Fuji'		Haplome A – 652; Haplome B – 650		
	Apple, 'M9'	2n=2x=34	Haplome A – 651; Haplome B – 650	Near-gapless	162
	Apple, 'MM106'		Haplome A – 643; Haplome B – 658		
<i>Malus domestica</i>	Apple, 'Golden Delicious'	2n=2x=34	GDT2T_hap1 – 650; GDT2T_hap2 – 644	T2T, pangenome	163
<i>Malus domestica</i>	Apple, 'WA 38'	2n=2x=34	HapA – 645; Hap B – 651	Chromosome-scale	164
<i>Malus hybrid</i>	Crabapple, SH6	2n=2x=34	HapH – 596; HapR – 649	Chromosome-level	165
<i>Malus hybrid</i>	Crabapple, 'Flame'	2n=2x=34	hapA – 688; hapB – 675		165
<i>Malus hybrid</i>	Crabapple, 'Royalty'	2n=2x=34	hapA – 674; hapB – 663	Chromosome-level	166
<i>Mangifera indica</i>	Mango, 'Irwin'	2n=2x=20	hap1 - 354; hap2 - 354		167
<i>Medicago sativa ssp. falcata</i>	Alfalfa, 'PI502453'	2n=4x=32	hap1 – 782; hap2 – 774; hap3 – 750; hap4 - 726	Pseudochromosomes	168
<i>Mentha suaveolens</i>	Mint, 'Variegata'	2n=2x=24	HapA – 401; HapB – 405		169
<i>Michelia alba</i>	Michelia (alloidiploid)	2n=2x=29	MC – 2100; MM – 2156	Chromosome-scale	170
<i>Mimosa bimucronata</i>	Mimosa	2n=2x=26	Haplotype A – 599; Haplotype B – 619	Pseudochromosomes	171
	Mulberry, 'ZS5801'		Hap1 – 301; Hap2 – 293		
<i>Morus alba</i>	Mulberry, 'ZB'	2n=2x=28	Hap1 – 309; Hap2 – 314	Chromosomal-level	172
<i>Myrciaria cauliflora</i>	Jaboticaba	2n=2x=22	Σ - 674	T2T	173
<i>Notholthocarpus densiflorus</i>	Tanoak	2n=2x=24	Hap1 – 840		174

Table 1, cont.

<i>Oryza longistaminata</i>	Wild rice	2n=2x=24	Hap1 – 358; Hap2 – 336	Chromosomal-level	175
<i>Oryza rufipogon</i>	Rice, Y476	2n=2x=24	Hap1 – 411; Hap2 – 412	T2T	176
<i>Phanera championii</i>	Champion's Bauhinia	2n=2x=28	Hap1 – 384; Hap2 – 383	Pseudochromosomes	177
<i>Phyllanthus emblica</i>	Indian gooseberry	2n=8x=104	Σ - 1820	Chromosomal-scale	178
<i>Sauropus spatulifolius</i>	Dragon's Tongue	2n=8x=103	Σ - 4880		
	Moso bamboo,				
	Accessions:		Haplotype 1 / Haplotype 2:		
	AJ		1970/1880		
	CS		1970/1910		
	CY		1980/1960		
	DA		1930/1900		
	HB		1980/1970		
	HS		1990/1940		
	HZP		1990/1970		
	JZ	2n=4x=48	1980/1940	Pangenome	179
	LY		2000/1930		
	RH		1980/1993		
	WYS		1980/1920		
	XA		1970/1940		
	XN		1990/1930		
	YA		1990/1950		
	YF		1920/1880		
	YX		2000/1900		
<i>Pinus densiflora</i>	Korean red pine	2n=2x=24	HA – 21738; HB – 21759	Chromosomal level	180
<i>Populus alba</i> × <i>P. tremula</i>	Hybrid poplar, '84K'	2n=2x=38	Subgenome A – 400; Subgenome B – 416	T2T, trio-binning	181
<i>Populus deltoids</i> × <i>P. euramericana</i>	Hybrid poplar, 'NL895'	2n=2x=38	Haplotype A – 377; Haplotype B – 378		182
<i>Populus tomentosa</i>	Poplar, 'GM107'	2n=2x=38	Σ - 715	Chromosomal level	183
<i>Prunus davidiana</i>	Wild peach	2n=2x=16	Pda_hap1 – 257; Pda_hap2 – 244	Chromosomes	184
<i>Prunus dulcis</i>	Almond, 'Texas'	2n=2x=16	Phase 0 – 254; Phase 1 – 252	Chromosomes	185
<i>Prunus pseudocerasus</i>	Chinese cherry, 'Zhuji Duanbing'	2n=4x=32	Hap1 – 246; Hap2 – 237; Hap3 – 225; Hap4 – 193	Pseudochromosomes	186
<i>Prunus salicina</i>	Plum, 'Fengtangli'	2n=2x=16	hap1 – 251; hap2 – 251	T2T	187
<i>Prunus zhengheensis</i>	Rare apricot	2n=2x=16	hap1 – 241; hap2 – 235	Chromosomal level, pangenome	188
<i>Pyrus communis</i>	Pear, 'd'Anjou'	2n=2x=34	Hap 1 – 388; Hap 2 – 393	Chromosome-scale	189
	Pear, 'Yuluxiang'		YLSA - 502; YLSXB - 499		
<i>Pyrus hybrid</i>	Pear, 'Hongxiangsu'	2n=2x=34	HXSA - 502; HXSB - 498	T2T, pangenome, trio-binning	190
<i>Rhododendron nivale</i>	Rhododendron	2n=4x=52	Σ four haplotypes – 2170	Pseudochromosomes	191

Table 1, cont.

<i>Rosa chinensis</i>	Chinese rose	2n=2x=14	HapA – 518; HapB – 541	Pseudochromosomes	192
<i>Rosa hybrida</i>	Rose, ‘Samantha’	2n=4x=28	∑ - Haplotypes A, B, C, D - 2151		193
<i>Saccharum</i>	Sugarcane, hybrid, ‘ZZ1’	2n=4x=114	∑ - 10380	Pseudo-chromosomes	194
<i>Salix babylonica</i>	Weeping willow, female	2n=4x=76	∑ - 1286		195
<i>Salix dunnii</i>	Weeping willow, male	2n=2x=38	∑ - 696	Chromosome-level	195
<i>Solanum commersonii</i>	Wild potato	2n=2x=24	Hap1 – 706; Hap2 – 711	T2T	196
<i>Solanum commersonii</i>	Wild potato	2n=2x=24	Hap1 – 707; Hap2 – 712		197
<i>Solanum okadae</i>	Wild potato	2n=2x=24	∑ - 699		198
<i>Solanum tuberosum</i>	Potato, ‘Altus’	2n=4x=48	∑ four haplotypes – 2925	Chromosomal clustering	199
<i>Stevia rebaudiana</i>	Candy/leaf	2n=2x=22	Haplotype A – 1100; Haplotype B – 1010	Chromosome assembly	200
<i>Trifolium repens</i>	White clover	2n=4x=32	Primary haplotig – 995; alternative haplotig – 1002	Chromosome-scale	201
<i>Vitis davidii</i>	Grape, ‘Föex’	2n=2x=38	Vd_H1 – 518; Vd_H2 - 513	Chromosome level	202
	Grape, ‘Manicure Finger’	2n=2x=38	MF_H1 – 489; MF_H2 - 486		
<i>Vitis vinifera</i>	Grape, ‘Chasselas’	2n=2x=38	Two haplo-genomes – 492 each	T2T	203
	Grape, ‘Ugni Blanc’	2n=2x=38	Two haplo-genomes – 497 each		
<i>Zingiber officinale</i>	‘Small Laiwu Ginger’	2n=2x=22	hap A – 1550; hap B – 1440	Pseudochromosomes	204
	Jujube var.spinoza, ‘SZ’	2n=2x=24	SZ_HapA - 413; SZ_HapB - 381		
<i>Zizifus jujuba</i>	Jujube, ‘Junzao’	2n=2x=24	JZ_HapA – 388; JZ_HapB - 390	T2T	205
	Indian jujube, ‘Misi’	2n=4x=48	cI – 391; cII – 391; cIII – 423; cIV – 424	T2T	206
<i>Ziziphus mariutiana</i>	Indian jujube, XSYS (wild)	2n=4x=48	wI – 422; wII – 421; wIII – 434; wIV – 434	T2T	

trio-binning – 9

gamete-binning – 4

pangenome – 7

Super-pangenome – 2

T2T - 30

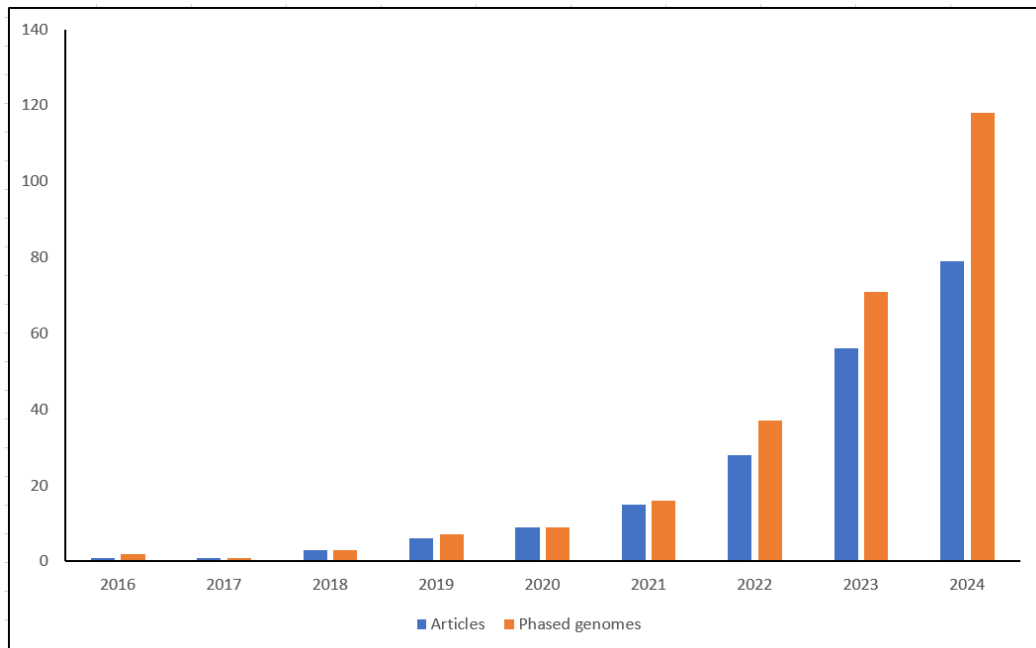


Fig. 1. The growing number of publications describing diploid plant genomes

As one can see in Table 1 and Figure 1, starting with a few articles in 2016–2017, rapid growth of such research began only in 2022. In 2024, 79 articles on phased genomes were published. By the end of 2024, diploid genomes from representatives of 143 species of higher plants belonging to 95 genera affiliated with 50 families were sequenced, and the results were published in 198 articles. As for diploid genomes for individual plant samples, their number by the end of 2024 was 258 because some articles provide data on multiple diploid genomes as well as about several plant species. Sizes of the assembled haplotypes of different plant species vary greatly, from 2×105 Mbp in *Arabidopsis thaliana* to more than 2×21 Gbp in *Pinus densiflora*, or ~ 200 -fold. Ploidy levels in plants with sequenced diploid genomes also vary, and there are diploid species (which are the majority) as well as triploid, tetraploid, hexaploid, several octaploid species, and even a nonaploid genome. The number of assembled chromosomes (from sequenced DNA) corresponding to diploid genomes (haplotypes) varies from 10 in *Arabidopsis* to 116 in the tetraploid species *Actinidia arguta* with base chromosome numbers 5 and 29, respectively. Many articles about different plant species show high heterozygosity of haplotypes. More information can be obtained from the original articles, which describe the haplotyped genomes of the species and samples listed in Table 1. Table 2 lists plant species with sequenced diploid genomes, arranged by family.

Below, we briefly summarize information about the diversity of species from different families for which diploid genomes have been sequenced. These include agricultural plants, fruit crops, medicinal plants, plants used in the pharmaceutical and perfume industries, large trees, endangered species, species of interest for understanding ongoing evolutionary events, and some others.

It is not surprising that the *Arabidopsis* model plant and grapes were among the first plants for which phased genomes were assembled [9]. Moreover, their complete quasi-genomes were also sequenced first and

fourth among higher plants, respectively. In general, diploid genomes have been determined for grapes from 28 samples, mainly of the *Vitis vinifera* species, as well as several wild grape species and some hybrids. In one of the papers, even a super-pangenome of the genus *Vitis* is composed [124]. It has been found that the dioecy characteristic of wild grape species was lost during domestication owing to a rare recombination event between male and female haplotypes [29].

From the family Rosaceae, 14 diploid genomes have been assembled for apple trees, including several varieties, as well as wild species and hybrids, which have enabled the creation of pangenomes for the species *Malus domestica* [22; 163]. Diploid genomes of many other fruit trees such as pears, peaches, apricots, almonds, and cherries, including hybrid forms, have been analyzed by sequencing in this family. Quite a large number of diploid genomes have been assembled for strawberry (9 accessions) including wild species and hybrids. Diploid genomes from roses and *Chaenomeles* from the same family have also been sequenced. Overall, diploid genomes of 37 specimens from genera *Cerasus*, *Chaenomeles*, *Fragaria*, *Malus*, *Prunus*, *Pyrus*, and *Rosa* have been assembled in Rosaceae. Pangenomes have been constructed for the species *Prunus zhengheensis* [188]. To assemble a phased genome of pear *Pyrus bretschneideri*, DNA from 12 pollen grains (gametes) has been sequenced, thereby allowing to obtain information about the features of recombination occurring during meiosis [16]. A comparison of the phased haplotypes with a reference genome has confirmed the mosaic structure of the latter, which, however, is not surprising. Meanwhile, those authors performed previously impossible analysis of allelic effects in pear gene expression with conventional quasi-haploid genome assembly [16]. After sequencing of 445 pollen grains, other authors assembled a phased diploid genome of apricot *Prunus armeniaca* at the pseudo-chromosome level with 99% accuracy [24].

The era of sequencing of their diploid genomes is coming

Table 2 - Taxonomy of species with diploid genomes

Family	Genus	Species
Gymnospermae		
Pinaceae	<i>Pinus</i>	<i>densiflora</i>
Angiospermae		
Monocotyledons		
Asparagaceae	<i>Asparagus</i> <i>Dracaena</i>	<i>kiusianus</i> <i>cambodiana</i>
Bromeliaceae	<i>Ananas</i>	<i>comosus</i>
Musaceae	<i>Musa</i>	<i>acuminata</i>
Orchidaceae	<i>Bletilla</i> <i>Vanilla</i>	<i>striata</i> <i>planifolia</i>
Poaceae	<i>Bambusa</i>	<i>odashimae</i>
	<i>Cynodon</i>	<i>dactylon</i>
	<i>Dendrocalamus</i>	<i>latiflorus</i>
	<i>Oryza</i>	<i>longistaminata</i> <i>rufipogon</i>
	<i>Panicum</i>	<i>milliaceum</i>
	<i>Phyllostachys</i> <i>Saccharum</i>	<i>edulis</i> <i>spontaneum</i>
Dicotyledons		
Actinidiaceae	<i>Actinidia</i>	<i>arguta</i>
		<i>chinensis</i>
		<i>eriantha</i>
		<i>latifolia</i>
Amaranthaceae	<i>Amaranth</i> <i>Suaeda</i>	hybrid <i>glaucua</i>
Amborellaceae	<i>Amborella</i>	<i>trichopoda</i>
Anacardiaceae	<i>Mangifera</i>	<i>indica</i>
Apiaceae	<i>Bupleurum</i> <i>Ligusticum</i>	<i>chinense</i>
		<i>chuanxiong</i>
Asteraceae	<i>Artemisia</i>	<i>annua</i>
	<i>Bidens</i>	<i>alba</i> <i>hawaiiensis</i>
	<i>Chrysanthemum</i>	<i>indicum</i>
	<i>Cosmos</i>	<i>bipinnatus</i>
	<i>Dahlia</i> <i>Stevia</i>	<i>pinnata</i> <i>rebaudiana</i>
Betulaceae	<i>Corylus</i>	<i>avelana</i>
Boraginaceae	<i>Ehretia</i>	<i>macrophylla</i>
Brassicaceae	<i>Arabidopsis</i> <i>Eutrema</i>	<i>thaliana</i>
		<i>japonicum</i>
Caryophyllaceae	<i>Dianthus</i>	<i>caryophyllus</i>
Cannabaceae	<i>Humulus</i>	<i>lupulus</i>
Chenopodiaceae	<i>Chenopodium</i>	<i>quinoa</i>
Convolvulaceae	<i>Ipomoea</i>	<i>batatas</i>
Coriariaceae	<i>Coriaria</i>	<i>nepalensis</i>
Cucurbitaceae	<i>Cucumis</i>	<i>melo</i>
Ebenaceae	<i>Diospyros</i>	<i>kaki</i>
Ericaceae	<i>Rhododendron</i>	<i>vialii</i>
		<i>nivale</i>
	<i>Vaccinium</i>	<i>corymbosum</i>
		<i>darrowii</i> <i>myrtillus</i>
Euphorbiaceae	<i>Manihot</i>	<i>esculenta</i>
Fabaceae	<i>Medicago</i>	<i>sativa</i>
	<i>Mimosa</i>	<i>bimucronata</i>
	<i>Phanera</i>	<i>championii</i>
	<i>Trifolium</i>	<i>pratense</i> <i>repens</i>
Fagaceae	<i>Castanea</i>	<i>sativa</i>
	<i>Notholithocarpus</i>	<i>densiflorus</i>
	<i>Quercus</i>	<i>glaucua</i> <i>rubra</i> <i>variabilis</i>
Hydrangeaceae	<i>Hydrangea</i>	<i>macrophylla</i>
Juglandaceae	<i>Carya</i>	<i>illinoensis</i>
	<i>Cyclocaria</i>	<i>paliurus</i>
	<i>Juglans</i>	<i>regia</i>
Lamiaceae	<i>Mentha</i>	<i>suaveolens</i>
Lauraceae	<i>Pogostemon</i>	<i>cablin</i>
		<i>americana</i>
Magnoliaceae	<i>Michelia</i>	<i>alba</i>
Malvaceae	<i>Firmiana</i>	<i>kwangsiensis</i>
	<i>Hibiscus</i>	<i>sabdariffa</i>
	<i>Microcos</i>	<i>paniculata</i>
Menyanthaceae	<i>Nymphoides</i>	<i>indica</i>
Moraceae	<i>Antiaris</i>	<i>toxicaria</i>
	<i>Ficus</i>	<i>carica</i>
	<i>Morus</i>	<i>alba</i>
Myrtaceae	<i>Eucalyptus</i>	hybrid <i>regnans</i>
	<i>Melaleuca</i>	<i>quinquenervia</i>
	<i>Myrciaria</i>	<i>cauliflora</i>
	<i>Syzygium</i>	<i>samarangense</i>
Oleaceae	<i>Chionanthus</i> <i>Jasminum</i>	<i>retusus</i> <i>sambac</i>
Papaveraceae	<i>Corydalis</i>	<i>yanhusuo</i>
Phyllanthaceae	<i>Fleuggea</i>	<i>virosa</i>
	<i>Phyllanthus</i>	<i>emblica</i>
	<i>Sauropus</i>	<i>spatulifolius</i>
Plantaginaceae	<i>Antirrhinum</i>	<i>hispanicum</i>
Polygonaceae	<i>Fagopyrum</i>	<i>esculentum</i> <i>tataricum</i>
	<i>Rheum</i>	<i>officinale</i>
Rhamnaceae	<i>Ziziphus</i>	<i>jujuba</i> <i>mariutiana</i>
Ranunculaceae	<i>Coptis</i>	<i>teeta</i>
Rosaceae	<i>Cerasus</i>	× <i>yedoensis</i> × <i>kanzakura</i>
	<i>Chaenomeles</i>	<i>specioza</i>
	<i>Fragaria</i>	× <i>ananasa</i>
		<i>chiloensis</i> <i>moupinensis</i> <i>virginiana</i>
	<i>Helianthus</i>	<i>tuberosus</i>

	<i>Malus</i>	<i>domestica</i> <i>fusca</i> hybrid
		<i>armeniaca</i> <i>avium</i> <i>dauidiana</i>
	<i>Prunus</i>	<i>dulcis</i> <i>pseudocerasus</i> <i>salicina</i> <i>zhengheensis</i>
		<i>bretschneideri</i>
	<i>Pyrus</i>	<i>communis</i> hybrid
	<i>Rosa</i>	<i>chinensis</i> hybrida
Rutaceae	<i>Citrus</i>	<i>australasica</i> <i>australis</i> <i>changshanensis</i> <i>glauca</i> <i>inodora</i> <i>limon</i> <i>sinensis</i>
	<i>Populus</i>	hybrid <i>tomentosa</i>
Salicaceae	<i>Salix</i>	<i>babylonica</i> <i>dunnii</i> <i>purpurea</i>

Sapindaceae	<i>Litchi</i>	<i>chinensis</i>
	<i>Capsicum</i>	<i>annuum</i>
Solanaceae	<i>Solanum</i>	<i>commersonii</i> <i>okade</i> <i>tuberosum</i>
Theaceae	<i>Camelia</i>	<i>sinensis</i> <i>oleifera</i>
	<i>Muscadinia</i>	<i>rotundifolia</i> <i>acerifolia</i> <i>aestivalis</i> <i>arizonica</i> <i>berlandieri</i> <i>girdiana</i> hybrid
Vitaceae	<i>Vitis</i>	<i>labruscana</i> <i>manticola</i> <i>mustangensis</i> <i>riparia</i> <i>rupestris</i> <i>vinifera</i> × <i>doaniana</i>
Zingiberaceae	<i>Zingiber</i>	<i>officinale</i>

Besides, after a sequencing analysis of 135 pollen grains, a diploid genome of tea *Camellia sinensis* from the family Theaceae was assembled [33]. Other tea varieties have also been analyzed by genome sequencing, just as the genome of tea oil camellia *C. oleifera*. Diploid genomes from the family Actinidiaceae have been sequenced in 13 samples of four species of *Actinidia chinensis*, *A. arguta*, *A. latifolia*, and *A. eriantha*, whose fruits are commonly known as kiwifruit. For the species *A. chinensis*, a pangenome has been compiled based on seven varieties [131].

Ten diploid genomes from the family Rutaceae have been assembled for different species of the genus *Citrus* and their hybrids: *C. australis*, *C. australasica*, *C. limon*, *C. sinensis*, *C. changshanensis*, *C. inodora*, and *C. glauca*. For many other taxa of fruit crops, diploid genomes have been assembled: persimmon, mango, avocado, lychee, mulberry, and one of the oldest known domesticated species: fig *Ficus carica*.

Considerable attention is given to tetraploid potato *Solanum tuberosum*, including a number of varieties, as well as wild diploid potato species *S. commersonii*, *S. okadae*, and *S. tuberosum*, for which a total of 15 diploid genomes have been sequenced. Among tetraploid potato taxa, *S. tuberosum* now has a pangenome

[64]. Diploid genomes of two *Capsicum annuum* specimens have been assembled from the same family. A diploid genome of sweet potato *Ipomoea batatas*, the seventh most important crop in the world, has been assembled from the family Convolvulaceae.

Diploid genomes for red and white clover from the family Fabaceae have been sequenced [68, 122], and a diploid genome of *Medicago sativa* has been assembled with haplotypes taking into account subgenomes [23]. A diploid genome of *Mimosa bimucronata* has been assembled, the analysis of which is focused on the mechanism of leaf movement and symbiotic nitrogen fixation [171]. Earlier, a diploid genome of the nonleguminous nitrogen-fixing plant *Coriaria nepalensis* has been sequenced [84].

Diploid genomes of ginger, hop, mint, and buckwheat have also been sequenced, which are plants used as staple human foods or as condiments as well as in food production. For representatives of seven genera of Asteraceae — *Artemisia*, *Bidens*, *Chrysanthemum*, *Cosmos*, *Dahlia*, *Helianthus*, and *Stevia* diploid genomes have been sequenced, and some of these plants have medicinal and nutritional significance, while the rest are ornamental flowering plants. Phased genomes of carnations, hydrangeas, and rhododendrons have also

been assembled for some ornamental plants from different families.

Many plants for which diploid genomes have been sequenced have been arousing interest because having a wonderful aroma or being medicinal, including those used in folk medicine, they are in demand in the perfume and pharmaceutical industries: jujube, bushweed, jasmine, patchouli, wild loquat, jaboticaba, rhubarb, and others. One of the plants of this group, *Corydalis yanhusuo* from the family Papaveraceae, has an unusual telomeric repeating motif: (TTTCGG)_n instead of the usual (TTTAGGG)_n [146]. By fluorescence *in situ* hybridization, those authors did not find such a motif in two species of the genus *Papaver* from this family, whereas the other five species of the genus *Corydalis* were found to carry it.

Sequencing in a phased haplotyped format of diploid genomes of dioecious plant *Asparagus kiusianus* belonging to male and female individuals can help to better understand the mechanisms that determine sex in such plants [48]. Haplotypes of dioecious plants have been assembled for two more willow species, male and female, *Salix babylonica* and *S. dunnii*, respectively [195]. Of particular interest is the sequencing of the diploid genome of nonvascular plant *Amborella trichopoda* and identification of sex-determining loci in this ancient plant, which is the only representative of a sister lineage toward other flowering plants [132].

Diploid genomes from woody plants have been sequenced for a large number of species from different families: eucalyptus, three species of oak, chestnut, some nuts, poplar, aspen, and some other trees. Diploid genomes of three bamboo species from the family Poaceae have been sequenced too. For moso bamboo *Phyllostachys edulis*, using diploid genomes of 16 specimens, a pangenome of this species has been constructed [179]. Diploid genomes of 12 more species belonging to 10 genera and four families, including important crops such as banana (Musaceae), pineapple (Bromeliaceae), sugarcane, and millet (both Poaceae), have also been assembled from the class Monocotyledonous. The diploid genome of *Vanilla planifolia* (from the family Orchidaceae), a producer of the well-known vanilla, has been sequenced.

It should be pointed out that almost all articles describing plant diploid genomes with phased haplotyped assembly emphasize the importance of establishing allelic states of certain genes for various purposes, including a better understanding of metabolic pathways, manifestations of heterosis, adaptability to adverse environmental factors, resistance to various pathogens, and domestication processes as well as for more accurate and effective further breeding of these taxa.

Conclusion

The cutting edge in the field of future whole-genome sequencing and even at present is the sequencing of phased (diploid) genomes at the chromosome level, from telomere to telomere, gap-free, or gapless. In fact, it can talk about the gradual advent of the era of diploid genome sequencing. In the meantime, in plants it is also important to know information about genomic diversity of crop varieties in the form of their pangenomes, which ensure, among other things, the manifestation of heterosis, in order to more thoughtfully involve various varieties and lines in breeding as well as to carry out genomic CRISPR/Cas editing based on knowledge of all gene alleles.

There is no doubt that many of the diploid genomes assembled so far, shown in Table 1, require further improvement (as indeed do most quasi-genomes, even as a conventional mosaic consensus assembly), but a phased assembly with even incomplete haplotype resolution is still better than a conventional consensus assembly, which carries inaccuracies, at least for predicted protein molecules. This problem can be critical. In addition, sequencing technologies and related software will undoubtedly continue to improve, which will make the assembly of haplotyped genomes easier and more accurate in the near future. At the same time, the sequencing of quasi-genomes will remain a thing of the past (because they do not carry important information about the functional state of organisms, including plants) and will be carried out only for species whose genomes have not yet been sequenced at all. Moreover, even pangenomes will have to be sequenced and assembled in a phased format because it is extremely important to see both different alleles and a hemizygous state of individual genes, which is not so easy to find out without the compiling of haplotypes.

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