Concepts and Strategies in Plant Sciences
Series Editor: Chittaranjan Kole

Liang Chen
Jie-Dan Chen *Editors*

The Tea Plant Genome

Springer

Concepts and Strategies in Plant Sciences

Series Editor

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Preface

The tea plant, *Camellia sinensis* (L.) O. Kuntze, originated in the southwestern part of China. Tea is the largest non-alcohol healthy beverage next to water in the world. According to the Annual Bulletin Statistics of International Tea Committee (2023), the tea plant has been cultivated in more than 50 countries with 5.32 million ha of plantation and 6.48 million tonnes of made tea in 2022. It is a very important cash crop for family income and social welfare in many countries, such as China, India, Sri Lanka, Turkey, Viet Nam, Kenya, Malawi, Japan, etc., and scientific research in tea plant is booming.

The tea plant is cross-pollinated, largely self-incompatible, with high heterozygosity, and a very large genome (~3.0 Gb), which has greatly hindered research and breeding in this crop. In recent years, modern genetic and genomic tools have contributed to the development of significant valuable resources for tea genetic improvement. Consequently, a book providing comprehensive and updated information on tea plant genomics and molecular breeding approaches is needed to fill a gap in the current literature on the tea plant. The chapter authors are top and highly reputed researchers in the field.

This book, *The Tea Plant Genome*, includes 20 chapters that cover the most relevant and hot topics in tea plant genetics and genomics. A first set of chapters includes its global economic and health importance, the botany and taxonomy, and main quality and functional components. A second group of chapters deals with genetics and breeding and includes genetic resources, commercial breeding, genetic transformation techniques, as well as the use of marker assisted-selection (QTL, GWAS). This is followed by a set of chapters on omics, including genomics, transcriptomics, metabolomics, proteomics, organelle genome, small RNA and DNA methylation. Two chapters are devoted to biotic and abiotic stresses, followed by two others focused on the SNP array and databases for molecular design breeding. Finally, a chapter deals with future perspectives in the omics era for tea breeding.

We hope that this book will be useful not only to the world tea community to enhance the understanding of tea genetics and omics, promote the progress of global tea breeding, and help us breed more desirable new tea cultivars to meet the demands

of different markets and consumers in the increasing world market, but also as a reference for other woody perennial species.

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Hangzhou, China Liang Chen
Hangzhou, China Jie-Dan Chen

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Liang Chen is a world-renowned professor in the Tea Research Institute of the Chinese Academy of Agricultural Sciences (TRICAAS) located at Hangzhou, China. He has extensive research experience in tea germplasm, genetics, breeding, and genomics. He received his Ph.D. in Tea Science from Zhejiang University, China, and had postdoctoral research from Cornell University, USA. He visited Ehime University in Japan, University of Florence in Italy, and Wageningen University and Research in the Netherlands as senior visiting professor. He has been appointed three times as Honorary Scientist and Advisor of the Rural Development Administration of the Republic of Korea. He has been the curator of the world's largest collection of tea genetic resources, National Tea Germplasm Repository at Hangzhou for 20 years and bred 3 dozens of national released and plant variety protection covered tea cultivars for the tea industry.

Jie-Dan Chen is an associate professor of tea genomics, genetics, and databases in the Tea Research Institute of the Chinese Academy of Agricultural Sciences (TRICAAS) located at Hangzhou, China. He has constructed a comprehensive database of genomic variations for molecular breeding in tea plants (TeaGVD).

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Abbreviations

1,2,6-TGG	1,2,6-tri-O-galloyl-β-D-glucopyranose
1,4,6-TGG	1,4,6-tri-O-galloyl-β-D-glucopyranose
2,4-D	2,4-dichloro phenoxy acetic acid
2-DE	Two-dimensional gel electrophoresis
3D	Three-dimensional
4CL	4-coumaric acid CoA ligase
A3SS	Alternative 3' splice site
A5SS	Alternative 5' splice site
AAO3	ABA aldehyde oxidase
AB	Apical buds
ABA	Abscisic acid
ABC	ATP-binding cassette
ABCC1-2	ABC transcripters
ABE	Adenine base editor
ABFs	Abre-binding factors
ACE	Angiotensin-converting enzyme
ACRs	Accessible chromatin regions
ACX	Acyl-CoA oxidase
AD	Anno domini
ADC	Arginine decarboxylase
ADH	Alcohol dehydrogenase
AEC	Anion exchange
AFLP	Amplified fragment length polymorphism
AGO	Argonaute
AI	Artificial intelligence
Al	Aluminum element
AlaDC	Alanine decarboxylase
Alt3	Alternative 3' splice site
Alt5	Alternative 5' splice site
AMADH	Aminoaldehyde dehydrogenase
AMY	α-amylase

ANN	Annexin
ANR	Anthocyanidin reductase
ANS	Anthocyanidin synthase
AOC	Allene oxide cyclase
AOs	Apoplastic ascorbate oxidase
AOS1	Allene oxide synthase 1
AP2	Apetala2
AP2/ERF	Ethylene-responsive transcription factors
APCI	Atmospheric pressure chemical ionization
APS	Aspartic proteases
APX	Ascorbate peroxidase
APX1	Cytosolic ascorbate peroxidase 1
AREBs	Abre-binding proteins
ARF	Auxin responsive factor
AS	Alternative splicing
AsA	Ascorbic acid
ASEGs	Allele-specific expression genes
ASMT	5-serotonin-N-acetyltransferase
AsODN	Antisense oligodeoxynucleotide
Asp	Aspartic acid
ATAC-seq	Assay for transposase accessible chromatin with high-throughput sequencing
B	Boron element
Ba	Barium
BADHs	Betaine aldehyde dehydrogenases
BAM	β-amylase
BDL	Below detectable limit
BE	Base editors
bHLH	Basic helix-loop-helix
BIN2	Brassinosteroid insensitive 2
BLC	Bud leaf color
BM	Bud mutation
BR	Brassinosteroid
BRI	Belt and Road Initiative
BRR	Bayesian ridge regression
BSP	Bisulfite treatment includes bisulfite sequencing PCR
BSR-Seq	Bulked segregant RNA-sequence
bZIP	Basic leucine zipper
C	(-)-catechin
C4H	Cinnamic acid 4-hydroxylase
Ca	Calcium element
CA	Cold acclimation
CA MTA	CaM-binding transcription activator
CAF	Caffeine
CALS3	Callose synthase 3

CaMs	Calmodulins
CAPS	Cleaved amplified polymorphic sequences
Cas	CRISPR-associated
CAT	Catalase
CBE	Cytosine base editor
CBF	C-repeat/DRE-binding factor
CBFs	C-repeat binding factors
CBLs	Calcineurin B-like proteins
CBPs	Ca^{2+}-binding proteins
CCaMK	Ca^{2+}/CaM-dependent protein kinase
CCoAOMT	Caffeoyl-CoA O-methyltransferase
CDPKs	Ca^{2+}-dependent protein kinases
CDPs	Catechin-derived peptides
CE-MS	Capillary electrophoresis-mass spectroscopy
CGIR	Chloroplast Genome Information Resource
CH	Controlled hybridized progenies
CHI	Chalcone isomerase
CHS	Chalcone synthase
CHXB	β-carotene hydroxylase
CI	Chemical ionization
CK	Cytokinin
CLR	Continuous long reads
CMLs	CaM-like proteins
CMT3	Chromomethylase 3
CNGCs	Cyclic nucleotide-gated channels
Co	Cobalt element
COLD1	Chilling tolerance divergence 1
COS	Chitosan oligosaccharide
CPD	Cytochrome P450 90A1
Cr	Chromium element
CRE1	Cytokinin receptor 1
CRISPR	Clustered regularly interspaced short palindromic repeats
CSA	*C. sinensis* var. assamica
CSD4	Cu/Zn-Superoxide dismutases4
CSDs	Cu/Zn-SODs
CSS	*C. sinensis* var. sinensis
CTD	C-terminal dimerization domain
CTR	Copper transporter
Cu	Copper element
CuAO	Amine oxidase
DA	De-acclimated
DAO	Diamine oxidase
DBD	DNA-binding domain
DCA	3,5-dichloroanthranilic acid
DCAPS	Derived cleaved amplified polymorphic sequences

DCL	Dicer-like
DEGs	Differentially expressed genes
DE-lncRNAs	Differentially expressed long ncRNAs
DEMs	Differentially expressed metabolites
DEPs	Differentially expressed proteins
DFR	Dihydroflavonol-4-reductase
DGE	Digital gene expression
DHAR	Dehydroascorbate reductase
DIA	Data-independent acquisition
DMNT	α-farnesene, β-Ocimene and (E)-4,8-dimethyl-1,3,7-nonatriene
DMTase	DNA demethylase
DNA	Deoxyribonucleic acid
Dof	DNA binding with one finger
DPE2	Disproportionating enzyme 2
DREBs	Dehydration-responsive element-binding proteins
DRM2	Domains rearranged methylase 2
DSBs	Double-strand breaks
DSGs	Differentially spliced genes
dsRNA	Double-strand RNA
DTBIA	Direct tissue blot immunoassay
DUS	Distinctness, uniformity, and stability
DXS1	1-deoxy-D-xylulose 5-phosphate synthase 1
EC	(-)-epicatechin
ECG	(-)-epicatechin gallate
ECP	Enzymatic-catalyzed processes
EGC	(-)-epigallocatechin
EGCG	(-)-epigallocatechin gallate
EI	Electron ionization
ELISA	Enzyme-linked immunosorbent assay
ENCODE	Encyclopedia of DNA elements
EPSFs	N-ethyl-2-pyrrolidinone-substituted flavan-3-ols
ER	Endoplasmic reticulum
EREB	Ethylene responsive element binding factor
ERF	Ethylene responsive factor
ES	Exon skipping
ESI	Electrospray ionization
EST	Expressed sequence tags
EST-SSR	Expressed sequence tag simple sequence repeat
ET	Ethylene
ETI	Effector-triggered immunity
eTMs	Endogenous target mimics
F_1	Filial 1
F3′,5′H	Flavonoid 3′,5′-hydroxylase
F3H	Flavanone 3-hydroxylase
FAAs	Free amino acids

FAIMS	Field asymmetric waveform ion mobility spectrometry
Fe	Iron element
FL	Flowers
FLS	Flavonoid synthase
FR	Young fruits
FRK	Fructokinase
FSDs	Fe-SODs
F_{ST}	F-statistic
FT	Fourier transform
FT-ICR-MS	Fourier transform on cyclotron resonance mass spectroscopy
GA	Gibberellic acid
GA20ox	GA 20-oxidase
GA2ox	GA 2-oxidases
GA2ox8	Gibberellin 2-oxidase 8
GA3ox	GA 3-oxidase
GABA	Gamma amino butyric acid
GAD	Glutamate decarboxylase
GAI	Gibberellin-insensitive
Gb	Gigabyte
GB	Glycine betaine
GBLUP	Genomic best linear unbiased prediction
GBS	Genotyping-by-sequencing
GC	(-)-gallocatechin
GCG	(-)-gallocatechin-3-gallate
GC-IMS	Gas chromatography-ion mobility spectrometry
GC-MS	Gas chromatography-mass spectroscopy
GCN	Gene coexpression networks
GC-O	GC-Olfactometry
GCs	Galloylated catechins
GDP	Gross domestic product
GEBVs	Genomic estimated breeding values
GLM	General linear model
Glu	Glutamate
GLVs	Green leaf volatiles
GolS	Galactinol synthase
GOPX	Guaiacol peroxidase
GP	Genomic predictions
GPX	Glutathione peroxidase
GR	Glutathione reductase
GRF1, 4, and 13	Growth-regulating factors 1, 4, and 13
GRX	Glutaredoxin
GS	Glutamine synthetase
GS FLX	Genome sequencer FLX system
GSH	Glutathione
GST	Glutathione s-transferase

GWAS	Genome-wide association studies
GWD	Glucan water dikinase
H	Heterozygosity
HAPs	Heme activator proteins
hc-siRNAs	Heterochromatic small interfering RNAs
HD	Heat-drought combined
HDAC19	Histone deacetylase 19
HDMF	4-hydroxy-2,5-dimethylfuran-3(2H)-one
HDR	Homology-directed repair
HD-ZIP III	Homeodomain-leucine zipper III
HESO1	Hen1 suppressor 1
HGT	Horizontal gene transfer
Hi-C	High-throughput chromosomal conformation capture
HILIC	Hydrophilic interaction chromatography
HIPVs	Herbivore-induced plant volatiles
HPL	Hydroperoxide lyase
HPLC	High performance liquid chromatography
HR	Hypersensitive response
HR-MS	High-resolution mass spectrometry
Hsf	Heat stress factors
HT	Heat
HTH	Helical-turned-helical
HXK	Hexokinase
HYL1	Hyponastic leaves 1
IAA	Indole-3-acetic acid
IBA	Indobutyrate
ICR	Ion cyclotron resonance
IGAE	Information gain attribute evaluation
ILP	Intron length polymorphic
IM-MS	Ion mobility mass spectrometry
InDel	Small insertion/deletion
INV	Invertase
IR	Intron retention
ISA3	Isoamylase
ISSR	Inter-simple sequence repeat
iTRAQ	Isobaric tag for relative and absolute quantitation
JA	Jasmonic acid
JAZ	Jasmonate Zim-domain
JMT	Jasmonic acid carboxyl methyltransferase gene
K	Potassium element
KASP	Kompetitive allele-specific polymerase chain reaction
KOR2	K PLUS_SPI outward-rectifying channel 2
KPIs	Kunitz-type protease inhibitors
Kub	Lysine ubiquitinated
LAC	Laccase

L-APX	L-ascorbate peroxidase
LAR	Leucoanthocyanidin reductase
LC-MS	Liquid-chromatography mass spectroscopy
LD	Linkage disequilibrium
LGs	Linkage groups
LIS1	Linalool synthase
LLE	Liquid-liquid extraction
lncRNAs	Long ncRNAs
LOX	Lipoxygenase
LP	Landraces or old tea seedling population
LRR-RLKs	Leucine-rich repeat receptor-like protein kinases
LSC	Large single copy
LTR	Long terminal repeat
MALDI	Matrix-assisted laser desorption/ionization
MAPK	Mitogen-activated protein kinase
MAS	Marker-assisted selection
MCS	Multi-cloning site
MDHAR	Monodehydroascorbate reductase
MeDIP	Methylated DNA immunoprecipitation
MeDIP-seq	Methylated DNA immunoprecipitation coupled with sequencing
MeJA	Methyl jasmonate
MEP	Methylerythritol phosphate
MeSA	Methyl salicylate
MEX1	Maltose excess1
Mg	Magnesium element
mg/g	Milligrams per gram
mg/kg	Milligrams per kilogram
miRISC	RNA-induced silencing complex
miRNA	MicroRNA
MITEs	Miniature inverted-repeat transposable elements
ML	Mature leaves
MLC	Mature leaf colors
MLS	Mature leaf shapes
MLT	Mature leaf texture
MLZ	Mature leaf size
Mn	Manganese element
MPSS	Massively parallel signature sequencing
MR	Middle region
MS	Mass spectrometry
MSAPs	Methylation-sensitive amplification polymorphisms
MSD	Mn-SOD
MST	Monosaccharide transporter
MVA	Mevalonic acid
Mya	Million years ago
MYB	Myeloblastosis
N	Nitrogen

NADP-ME	Nicotinamide adenine dinucleotide phosphate-dependent malic enzyme
NBS-LRR	Nucleotide-binding site with leucine-rich repeat
NCED	9-cis-epoxycarotenoid dioxygenase
ncRNAs	Non-coding RNAs
NES	Nerolidol synthase
NFY	Nuclear transcription factor Y
NF-Y	Nuclear factor Y
NGCs	Nongalloylated catechins
NGDC	National Genomics Data Center
NGS	Next-generation sequencing
NHEJ	Non-homologous end-joining pathway
Ni	Nickel element
NLRs	Leucine-rich repeat receptors
NLS	Nuclear localization signal
NMR	Nuclear magnetic resonance spectroscopy
NMT	N-methyltransferases
NO	Nitric oxide
NSC	Nonstructural carbohydrates
OAVs	Odor activity values
OL	Old leaves
ONT	Oxford nanopore technologies
OP	Open pollinated progenies
OP/INT	Open pollinated seeds introduced from other countries
OS2	β-Ocimene synthase
OTV	Off-target variants
P	Phosphorus element
P5CR	Pyrroline 5-carboxylate reductase
P5CS	Pyrroline 5-carboxylate synthetase
PAL	Phenylalanine ammonia lyase
PAMPs	Pathogen-associated molecular patterns
PAO	Polyamine oxidase
PBR	Plant breeder's rights
PCA	Principal component analysis
PCD	Host-programmed cell death
PCR	Polymerase chain reaction
PCS1	Phytochelatin synthase
PD	β-Primeverosidase
PE	Prime editor
PEG	Polyethylene glycol
PGC	Porous graphitic carbon
phyB	Phytochrome B
PIC	Polymorphic information content
PIF	Phytochrome interacting factor
PI-PLC	Phosphoinositide-specific phospholipase C
piRNAs	Piwi-interacting RNAs

PLD	Phospholipase D
PLS-DA	Correlation analysis, partial least squares-discriminant analysis
POD	Peroxidase
Pol II	RNA polymerase II
POX	Peroxidase
PP2C	2C protein phosphatase
PPO	Polyphenol oxidase
PR	Pathogenesis-related
pre-mRNA	Precursor mRNA
pri-miRNAs	Primary miRNAs
Pro	Proline
PRRs	Pattern recognition receptors
PrxR	Peroxiredoxin
PSY1	Phytoene synthase 1
PTI	Pathogen-associated molecular patterns-triggered immunity
PTMs	Posttranslational modifications
PVP	Plant varieties protection
PWD	Phosphoglucan water dikinase
QC	Quality control
QTL	Quantitative trait loci
RAD-seq	Restriction-site associated DNA sequencing
RAPD	Random amplified polymorphic DNA
RdDM	RNA-directed DNA methylation
RDRs	RNA-dependent RNA polymerases
RGA	Repressor of ga1-3
RGA1	G-protein α subunit 1
RICE1	Risc-interacting clearing 3'-5' exoribonuclease 1
RISC	RNA-induced silencing complex
RLK-LRR	Receptor-like kinases with LRR domain
RLM	RNA ligase-mediated
RM	Radiation mutation
RNA-seq	RNA sequencing
ROS	Reactive oxygen species
RP	Reversed-phase
RS	Raffinose synthase
RT	Tender roots
RT-LAMP	Reverse transcription loop-mediated isothermal amplification
RT-qPCR	Real-time quantitative PCR
RWC	Relative water content
S	Sodium element
SA	Salicylic acid
SAGE	Serial analysis of gene expression
SAMT	Salicylic acid carboxyl methyltransferase
SBP	S-RNase binding protein
SCL	Scarecrow-like
SCoT	Start codon targeted

SCPL	Serine carboxypeptidase-like
scRNA-seq	Single-cell RNA sequencing
SCT	Sum of caffeine and theobromine
SCX	Strong cation exchange
Se	Selenium element
SE	Serrate
Sect. Thea	Section Theaceae
SEX4	Phosphoglucan phosphatase starch excess 4
SHH1	Sawadee homeodomain homologue 1
siRNA	Small interfering RNA
SKI2	Superkiller2
SKOR2	Stelar K^+ outward rectifier
SLAF seq	Specific location amplified fragment sequencing
SLE	Solid-liquid extraction
SM	Secondary metabolite
SMRT	Single-molecule real-time sequencing
SNAT	Serotonin-N-acetyltransferase
SNP	Single nucleotide polymorphism
SnRK1	Suc-nonfermenting1-related protein kinase 1
SOD	Superoxide dismutase
SOS	Salt-overly-sensitive
SP	Self-pollinated progenies
SPE	Solid-phase extraction
SPL-3	Squamosa promoter-binding-like protein
SPP	Sucrose phosphate phosphatase
SPS	Sucrose-phosphate synthase
SqRT-PCR	Semi-quantitative reverse PCR
SRAP	Sequence-related amplified polymorphism
SS	Phosphorylases, limit dextrinase, starch synthase
SSC	Small single copy
SSR	Simple sequence repeat
ssRNA	Single-strand RNA
ST	Young stems
STK1	Ser/Thr-protein kinase
SUS	Sucrose synthase
SUT	Suc transporter
SVM-FS	Support vector machine feature selection
T2T	Telomere-to-telomere
T5H	Tryptophan hydroxylase
TALENs	Transcription activator-like effector nucleases
TBCs	Tea bioactive compounds
TBF	Timing of spring bud flush
TBR	Theobromine
TBs	Theabrownin
TC	Total catechins
TCS1	Tea caffeine synthase 1

TDC	Tryptophan decarboxylase
TF	Transcription factor
TFs	Theaflavins
Thea	Theanine
TI	Terpene index
Ti	Titanium element
TIC	Total ion chromatogram
TLP	Thaumatin-like proteins
TMT	Tandem mass tag
TMV	Tobacco mosaic virus
TOF	Time of flight
TOF-MS	Time-of-flight mass spectroscopy
TPP	Trehalose-6-phosphate phosphatase
TPs	Tea polyphenols
TPS	Trehalose-6-phosphate synthase
TRAP	Target region amplified polymorphism
TRIC	Trihydroxylated catechin
TRs	Thearubigin
TRV	Tobacco rattle virus
TS	Theanine synthetase
TSA	Tryptophan synthase α-subunit
TSB2	Tryptophan synthase β-subunit
UDP	Uridine diphosphate
UGT	UDP-glycosyltransferases
UGT85A53	Uridine diphosphate-glucosyltransferase
UHPLC	Ultra-high pressure liquid chromatography
UHRMS	Ultra-high resolution mass spectrometry
UPS	Ubiquitin-26S proteasome system
URT1	Uridylyl transferase 1
UTRs	Untranslated regions
VIGS	Virus-induced gene silencing
VOCs	Volatile organic compounds
VTs	Volatile terpenes
WES	Whole-exome sequencing
WGBS	Whole-genome bisulfite sequencing
WGCNA	Weighted gene co-expression network analysis
WGD	Whole-genome duplication
WGRS	Whole-genome re-sequencing
WGS	Whole genome sequencing
WOX	Wuschel-related homeobox
YL	Young leaves
ZA	Zeatin
ZEP	Zeaxanthin epoxidase
ZFNs	Zinc-finger nucleases technology
Zn	Zinc element
μg/g	Micrograms per gram

Chapter 1
Tea Plant: A Millennia-Old Cash Crop for a Healthy and Happy Life Worldwide

Chang-Jian Pan, Xu-Lin Yang, and Liang Chen

1.1 Introduction

As an ancient crop, the tea plant has a long history and diverse cultural backgrounds. Tea is a popular drink with rich nutritional health benefits that bring many advantages worldwide. This section introduces the origin and spread of tea plants and then provides an analyses of the current situation of the global tea industry, including planting, production, and trade, and the importance of the tea industry to life and international exchange of tea.

1.2 The Center of Origin and Dissemination of Tea Plants

There is great interest in the scientific issues related to the origin and birthplace of the tea plant, and the origins of the tea plant have been explored from many historical sources and its geological heritage. The overall consensus is that the tea plants was discovered long ago and has been utilized for thousands of years. The home of the tea plant is the southwestern region of China, specifically Yunnan province.

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1.2.1 The Origins of Tea Plants

Origin is the natural process from zero to one. Evolution is the process from less to more and from simple to complicated. It is a challenge to explore the origin of tea plants. Historical traces and evidence do however provide substantial support for the origin of tea plants, allowing people to understand and explore it in depth and from various perspectives. With the continuous development of scientific technology, this question has gradually received scientific conclusions (Chen and Yang 2011).

According to Chen (1994), tea plants evolved from *Camellia* species, and *Camellia sinensis* appeared 40 million years ago. Analysis by botanists found that the origin of tea plants was 60–70 million years ago (Yao and Chen 2012).

The origin of tea plant is the distribution area before its domestication. There is more evidence to support the claim that the tea plant originated in China than the claim of Indian origin (CTSS 2022). Some scientists believe it is the same as the original center. The origination of tea plants from China has been acknowledged as being the case for a long period of time. A dispute was raised after a so-called wild tea plant was found to have originated from India in 1824. Actually, there are no real "wild tea plants" in Assam, India. A renowned taxonomist, Chang (1981), reported that, following careful investigation, the tea plant in India was the same as the widely distributed and cultivated large leaf tea plants in Yunnan province, China.

Tea plants originated from China. Only, there are different views about the actual origination center. A world-famous taxonomist of Theaceae and other families, Chang (1981), reported that over 90% of the genus *Camellia* species distributed in the southwest and south of China, centered on the Tropic of Cancer along Yunnan, Guangxi and Guangdong provinces, the adjacent area of Yunnan, Guangxi, and Guizhou provinces. So, this adjacent area is considered the original center for the genus *Camellia* species. Wild tea plants were first discovered in Yunnan Province in southwestern China, where abundant and diverse wild tea plants were found growing in the primeval forest (Yu 1986). Yu also found that Yunnan is the origin of tea plants according to the results of tea germplasm investigation, the theory of species origin, the quantity of species, the discovery of new species, the regularity of horizontal and vertical species distribution, and the morphological characterization of species in Sect. *Thea* (L.) Dyer in Yunnan. Yu further indicated that the long-narrow region of Wenshan and Honghe cities (southeast of Yunnan, China), located at 22°40′–24°10′ N, 103°10′–105°20′, is the original center for tea plants, based on the geological history and concentrated distribution of primitive species of sect. *Thea* in the southeast of Yunnan, China. Another famous taxonomist of Theaceae, Min (2000), pointed out the Sect. *Thea* is evolved from sect. *Archecamellia* Sealy. The subtropical limestone area of southeast of Yunnan, west of Guangxi, and southwest of Guizhou is the original center of Sect. *Thea* plants. In further studies, Yunnan is believed to be the original center of tea plants, based on Yunnan having high levels of species diversity of tea plants (wide distribution of tea plants and its wild related species) (Chang 1981; Yu 1986; Min 2000); high levels of phenotypic diversity (Yu 1986); *Chinese Tea Encyclopedia* shows that China possesses the largest number of

wild tea plants and the richest genetic diversity of tea germplasm resources, and southwestern China has the most *Camellia* plants. Among them, Yunnan tea plants [*Camellia* L. Sect. *Thea* (L.) Dyer] have the most species, the richest variants, and the closest affinity to *Camellia* spp. (Chen and Yang 2011). Yunnan tea plants also exhibit high levels of biochemical component diversity (Jin et al. 2014), high levels of DNA genetic diversity (Yao et al. 2012), and, in particular, whole genome level diversity (Wang et al. 2020).

In conclusion, the southwest of China, specifically Yunnan, is the original center of tea plants.

1.2.2 The Dissemination from the Origin to the Rest of the World

The spreading of tea plants includes the spreading from the original center Yunnan to other tea-growing places in China, the dissemination from China worldwide, and the spread of tea from China to the world.

1.2.2.1 From the Origin to the Other Parts of China

Chemical experiments and DNA marker tests have demonstrated transmission routes from Yunnan province, Guangxi Zhuang Autonomous Region, and other tea-growing regions in China. Yao et al. (2012) used simple sequence repeat (SSR) DNA markers to analyze the genetic diversity of 450 accessions of Chinese core tea germplasms. The genetic diversity (*H*) and polymorphic information content (PIC) decrease as the distance from the center of origin (Yunnan province and the neighboring Guangxi) toward the north and east regions increases. Lower allele numbers, *H* and PIC, are observed as being farther away from Yunnan and Guangxi provinces.

The ratio of linalool and geraniol (terpene index, $TI = \frac{(\text{Linalool} + \text{Linalool oxides})}{(\text{Linalool} + \text{Linalool oxides}) + \text{Geraniol}}$) in tea volatiles was used to explain the origin and dispersion of tea plants (Tadakazu et al. 1992). The tea plants growing in Yunnan province, which is proposed as the original center of tea plants, had a TI of near 1.0, and the TI of tea plants in the rest of China decreased gradually from near 1.0 in Yunnan to very low in the east of China. They proposed four possible dispersion routes of tea plants from Yunnan to other parts of China: (1) spreading along the sea, from Yunnan to Guangxi, Guangdong, Fujian to Zhejiang, (2) dispersing from Yunnan via Sichuan to Shaanxi, (3) spreading from Yunnan, via Sichuan, Hubei, to Anhui and Jiangsu along the Yangtze River, and (4) dispersing from Yunnan via Sichuan to Guizhou, Hunan, Jiangxi, and Zhejiang.

The path of the spread of tea plants from southwestern regions to Jiangxi, Zhejiang, and Fujian provinces can also be corroborated from the perspective of

historical and cultural transmission. In this process, Taoism and Buddhism played an important role in the spread. According to the *Chinese Tea Encyclopedia*, Taoist priests and monks brought tea from Yunnan to Sichuan and Jiangxi among other places.

1.2.2.2 From China to the Rest of World

Chinese tea planting techniques and tea processing technologies have gradually spread to other parts of the world. From China, the tea plants spread to other Asian countries, as well as to Africa, Europe, and the Americas, and adapted to local climatic and soil conditions, developing distinctive varieties of tea. During the Sui dynasty in China, tea was introduced to Japan by Buddhist monks. Tea use spread during the sixth century AD (Kiple and Ornelas 2000). During the twentieth century, tea plants and the production technology were distributed to Africa and other parts of Asia, such as Guinea, Mail, Algeria, Pakistan, etc., by the Chinese government (Chen and Yang 2011; Ma and Chen 2018). The main force and channel through which the tea plant spread to other countries and regions, besides royalty and religion, was via ancient traders. They brought tea seeds and tea, ceramics and silk, etc., to other countries in the world along the land-based and also sea-based Silk Road.

1.3 The Worldwide Tea Industry

The tea industry is a global industry, and many countries or regions have been involved in tea planting, production, and trade, and even some countries or regions that have never planted tea before have begun to develop a tea industry. The tea industry occupies an important position in the economy of some countries and has also become an important link for socioeconomic cooperation among the countries concerned. The tea industry has an important role to play in the global socioeconomic development of quality.

1.3.1 Global Tea Planting and Production

To 2022, the world's tea plantation area reached 5318 kilo-hectare. According to the Annual Bulletin of International Tea Committee (ITC 2023), the top ten countries and regions with the largest tea planting areas in 2022 were China (Mainland), India, Kenya, Sri Lanka, Vietnam, Indonesia, Myanmar, Turkey, Bangladesh, and Uganda, accounting for 94.19% of the world's tea acreage (Fig. 1.1).

To 2022, total global tea production reached 6477 kilotons, an increase of 1456 kilotons compared to 2013. The top ten countries and regions of tea production in

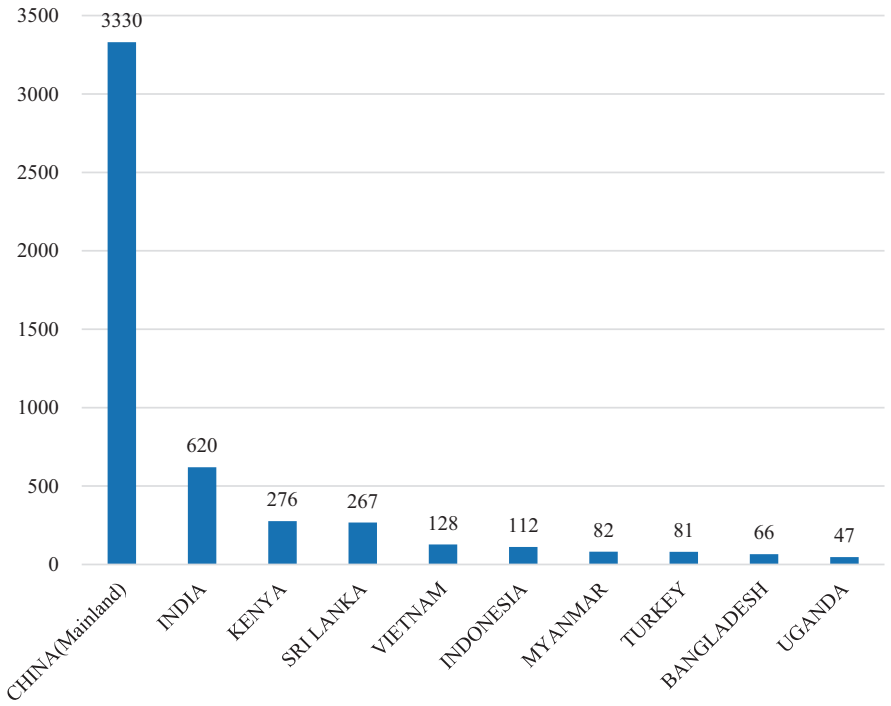

Fig. 1.1 Top ten countries and regions of tea plantation in 2022 (kilo-hectare). (Data source: Annual Bulletin of International Tea Committee 2023)

2022 were China (Mainland), India, Kenya, Sri Lanka, Turkey, Vietnam, Indonesia, Bangladesh, Uganda, and Argentina (see Fig. 1.2).

The countries and regions of the world producing tea were mainly in Asia and Africa. Tea production and its share in each continent are shown in Fig. 1.3. Asian countries are the major players and contributors to the global tea industry. The major tea-producing countries and regions in Asia include China, India, and Sri Lanka. China is the home of tea and has vast tea-producing regions. Major tea-producing provinces include Fujian, Zhejiang, Anhui, Yunnan, Guizhou, Sichuan, and Hubei. India is the second largest tea producer in the world, with major producing areas including Assam, Darjeeling, Kangra, and Nilgiris. Sri Lanka is an important tea exporting country, with the main producing areas located in the central highland and southern inland areas of the island. Bangladesh is located in the South Asian subcontinent, neighboring Myanmar and India. The country produces mainly black tea and, to a lesser extent, green tea in Moulvibazar and Habiganj which are the main producing areas. Turkey is now one of the most important tea producers in the world; all tea gardens in Turkey are established through seedlings and show great heterogeneity. The tea industry in Turkey consists of black tea production and a small amount of green tea, mixed with some fruits. In addition, tea improvement activities which concentrate on clonal selection to decrease seedling populations