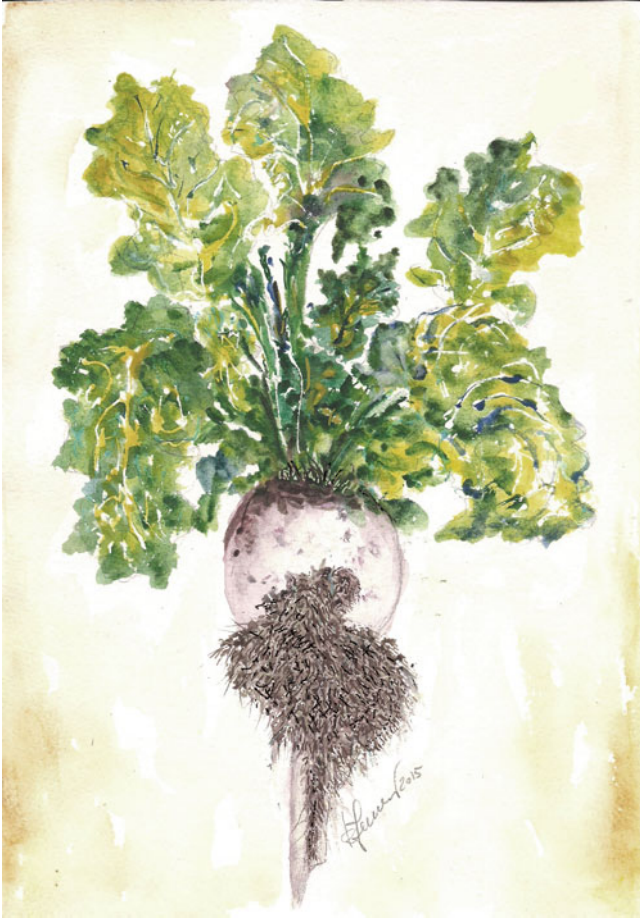


Enrico Biancardi · Tetsuo Tamada
Editors

Rhizomania

 Springer

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Enrico Biancardi
Stazione Sperimentale di Bieticoltura
Rovigo, Italy

Tetsuo Tamada
Agricultural Research Institute
Hokuren Federation of Agricultural
Cooperatives
Naganuma, Hokkaido, Japan

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“To my wife Donatella, who accepted to spend her life not only with me but also with the genus Beta”

—Enrico Biancardi

“To my wife Sachiko and my daughters Machiko and Chieko who gave warm support to my BNYVV work”

—Tetsuo Tamada

Foreword

An unknown disease of sugar beet was detected in Italy more than 50 years ago. Soon the new syndrome displayed devastating effects on yield. This greatly concerned the Italian sugar beet growers and processors, especially considering that the syndrome had spread to the most important Italian cultivation areas.

It was the start of a memorable enterprise for pathologists, breeders, and agronomists. The spontaneous and unusual synergy created among the universities, research stations, seed companies, and grower associations led not only at the first very appropriate attempts of prophylaxis measures but also to an awareness that the only possible management would be through the use of resistant varieties. In this phase, the *Beta maritima* germplasm selected at Rovigo and later at Salinas began to display its value against the new disease called “rizomania.” Some resistant varieties were released, thanks to enhanced knowledge of the pathogenic agents (beet necrotic yellow vein virus and *Polymyxa betae*) obtained in Japan and Germany.

It also was the beginning of countless research projects and collaborations worldwide, which, in a relatively short time, led to almost complete control of the disease. There are perhaps few other diseases, even affecting more important crops, on which so many papers have been published. It should be noted that the most significant results in the discovery of rhizomania resistance traits were obtained by public research stations, often without any specific funding.

The future of sugar beet currently is endangered by the development of resistant strains in the virus, among other things. I believe that it also will be possible to overcome these new obstacles with the help of the powerful tools provided by molecular investigation and following the knowledge carefully collected in this very useful book, the first devoted exclusively to rhizomania.

The issue was much more difficult 50 years ago, when no one knew anything about the syndrome and the researchers only had their eyes to see, a microscope to look closer, and a pencil to take notes.

Alma Mater Studiorum
Bologna, Italy
May 2016

Antonio Canova

Preface

This book is the result of an international enterprise among researchers involved in past and present studies on rhizomania, a relatively new and devastating disease of sugar beet. In less than 50 years, the disease has become the most damaging biotic factor affecting the crop worldwide. Moreover, its spread is still ongoing in every cultivated area. Because the traditional management systems were almost ineffective, it was soon evident that the employment of genetic resistances was the only chance for limiting the economic damage. The discovery of the pathogenic agents and the release of the first resistant varieties are described by some of the researchers directly involved.

The breeding efforts led to both the current satisfactory management of the disease and to the survival of the beet sugar industry in several areas. The cooperation between the Italian and American Experimental Stations, born spontaneously about 80 years ago and still continuing today, should be remembered. The friendly collaboration led to the employment of genetic traits extracted from *Beta maritima*, which became the sole source so far of the resistances available against the disease.

The introduction briefly describes sugar beet cultivation, the more common diseases, and the damage caused by rhizomania. This is necessary because the book also is addressed to readers who are not directly involved with sugar beet. Without these brief explanations, some parts of the text would not be fully comprehensible. The following chapters refer to the molecular physiology of the disease agents and their interactions with the environment and the host-plant. The knowledge of ecology and epidemiology of rhizomania is, above all else, necessary to understand the means and practices valuable to avoid or at least delay the further spread of the disease into healthy soils. Some promising methods of control using concurrent but not damaging viruses, bacteria, and fungi are in progress. They could help the action of the genetic resistances, which are not completely effective. The integrated protection is useful, especially in the even more frequent occurrences of resistance-breaking strains of BNYVV, where the known types of resistance seem to have partially lost their original efficacy. Some almost immune transgenic varieties are already awaiting release. For traditional breeding, further efforts will be needed in

search of new resistances in the wild species of the genus *Beta*. The availability of large collections of *Beta* germplasm collected all over the world should ensure further success in this direction. The target will be gained by means of conventional selection methods, assisted by updated techniques for genome analyses. Finally, perspectives are described to not only reduce the current damages but also to avoid further spread and noxious evolutions of rhizomania agents.

By means of interdisciplinary approaches, this book was edited above all to provide a broad, comprehensive, and updated overview of the various aspects of rhizomania, now scattered in countless publications. The outlook should be valuable for farmers, extension services, students, and researchers committed to ensuring the future of the sugar beet crop.

Rovigo, Italy
Naganuma, Japan

Enrico Biancardi
Tetsuo Tamada

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Antonio Canova must be recognized for his encouragement and convincing and enthusiastic support of this enterprise. The editors are grateful to Bob Lewellen, Lee Panella, and Mitch McGrath for their contributions and critical reading and revisions of the text and proofs. Special thanks go to Piergiorgio Stevanato for his help in translating and organizing the manuscript. Together with Mauro Colombo, he collaborated on the digital drawing of tables and figures. Many thanks are also addressed to Kelley Richardson for editing Chap. 12. Loving thanks are given by Biancardi to his wife for the original watercolor printed in the first pages of the book. Tamada is grateful to his colleague Hideki Kondo for generous help with tables and figures in parts of this book. His long-term research on rhizomania was carried out at Hokkaido Central Agricultural Experiment Station and Institute of Plant Science and Resources, Okayama University, and financially supported by Hokkaido Sugar Beet Associations.

The editors express also their gratitude to the numerous colleagues for the confidence given when the prospects for this book were still in the early stages of discussion and development. Finally, grateful memory must be addressed to the Italian researchers who firstly contributed both to the discovery of the disease agents and to plant-host resistance, which allowed survival and development of the sugar beet crop and the connected sugar industry.

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Author's Contributions to Rhizomania Research

Michael J.C. Asher Studied the ecology and epidemiology of *Polymyxa betae* and sources of resistance in wild *Beta* species, identifying two genes carrying the trait. Contributed to models predicting the development and spread of rhizomania and to the development of molecular markers for novel sources of resistance.

Enrico Biancardi Classified as “Alba type” the multigenic rhizomania resistance carried by old Italian genotypes. Collected sea beet populations in the Po River Delta, from which new sources of resistance were identified and developed. Lead author and editor in books, reviews, papers on aspects of research on rhizomania and *Beta maritima*.

Antonio Canova In 1966, hypothesized the connection “virus A”-*Polymyxa betae* as cause of the “low sugar content syndrome”. *Polymyxa betae*, identified and classified a few years before by Keskin, plays the role of carrier, while the real pathogen is the virus. He named the disease “*rizomania*”, later anglicized to rhizomania.

Sotaro Chiba Collaborated with Tamada and identified amino acids of the p25 protein for induction of the resistance response in leaves of *Beta vulgaris* and found function of the p25 protein as an avirulence factor. He analyzed worldwide isolates of BNYVV and obtained information on the global biogeography, evolution, virulence, and spread of BNYVV.

Marco De Biaggi In 1978, together with Biancardi, discovered and selected rhizomania resistance traits in cercospora leaf spot resistant genotypes. In 1985, released the first monogenic resistant variety endowed with the “Rizor type” resistance. He was among the first to apply ELISA techniques in screening beets for mass selection. In collaboration with Stevanato and Biancardi, he recently verified the similarity between the resistances Rizor and Holly (Rz1).

David Gilmer Studies molecular biology of BNYVV looking for RNA and protein structure-function relationships. Aims to understand BNYVV viral cycle.

Luciano Giunchedi Collaborated with Canova on the etiology of rhizomania, and later with De Biaggi in characterizing the mechanisms of the Rizor resistance in reducing the damages caused by BNYVV.

Hideki Kondo Collaborated with Tamada since 1995. He studied with Andika the molecular mechanisms of RNA silencing in roots and root-specific suppression of RNA silencing. He analyzed genetic diversity of BNYVV and evolution of benyviruses, and discovered benyvirus replicase-related sequences integrated into the genomes of diverse eukaryotic organisms.

Robert T. Lewellen Determined inheritance and named the gene *Rz* (the “Holly type” resistance) after discovery by Erichsen and his subsequent release of the variety “Rhizosen” in 1990. Resistance to BNYVV was found in *Beta maritima* accessions collected in Europe. Released lines, as C48, C79, and R740, were used internationally to identify *Rz2*, *Rz3*, *Rz4*, and *Rz5* and incorporated into commercial resistant varieties. With Wisler devised disease severity scale and its correlation with concentration of BNYVV. More recently, with Liu, discovered evidence of resistance-breaking strains of BNYVV and used *Beta macrocarpa* as systemic host to incorporate specific virus strains with *Polymyxa betae*. With Biancardi and Panella, published extensively on rhizomania research and resistance, particularly from *Beta maritima*.

J. Mitchell McGrath Has a long-standing interest in the genetics, genomics, and germplasm enhancement of sugar beets. He actively releases sugar beet germplasm with novel genetic characters and investigates the organization of the beet genome. Resistance gene structure and function, including rhizomania genes, is a recent interest afforded by a complete genome sequence.

Peyman Norouzi Identified some molecular markers linked to rhizomania resistance genes and selected many pollinators, OType lines, and populations accordingly. He co-authored papers published by Stevanato regarding the identification of SNP markers linked to rhizomania resistance genes. He collaborated to develop transgenic lines resistant to rhizomania and other traits.

Leonard W. Panella In collaboration, with Biancardi and Lewellen, co-authored the book “*Beta maritima*: the origin of beets”. Collected seed of *Beta maritima* and other wild beets, including *Beta nana* and *Beta patellaris* (*Patellifolia patellaris*), in many parts of the world. In collaboration with Stevanato and colleagues, developed molecular genetic markers for resistance to BNYVV. Developed enhanced germplasm that combined resistances to rhizomania, cercospora leaf spot, and rhizoctonia root rot.

Claudio Ratti Studied the epidemiology of BNYVV in Italy and in Europe developing molecular methods for detection and characterization of BNYVV types. Together with Gilmer, currently studies the biology of members of family

Benyviridae by reverse genetic approach with particular attention to BNYVV and beet soil-borne mosaic virus (BSBMV).

George N. Skaracis and **Ourania I. Pavli** Authored several publications regarding conventional and molecular breeding methods, with emphasis on genetic engineering, to develop durable rhizomania resistance.

Piorgiorgio Stevanato Collected seed of sea beet populations in the countries bordering the Adriatic Sea. Authored several publications together with Panella, Lewellen, Biancardi, De Biaggi, Pavli, and Skaracis. Improved the molecular methods for identifying and more rapidly increase the resistances to rhizomania, bolting, fusarium yellows, and *Heterodera schachtii*.

Tetsuo Tamada Identified the causal agent of rhizomania and named it “beet necrotic yellow vein virus” (BNYVV) in 1973. Since then, he worked with many colleagues on the characterization of virus, vector transmission, detection and diagnosis, ecology, and control. In 1995, he moved to Institute of Plant Science and Resources of Okayama University and continued to work on biological and molecular properties of BNYVV. Identified viral genes involved in vector transmission, disease development, and genetic resistances. Published extensively on the results.

Abbreviations

2x, 3x, 4x (or 2n, 3n, 4n)	Diploid, triploid, tetraploid genotypes
A	Alanine
aa	Amino acids
AD	Activation domain
AGO	Agonotute
AK	Alkalinity coefficient
AMOVA	Analysis of molecular variance
ANB	Italian Sugar Beet Growers Association
ARS	Agricultural Research Service
ASSBT	American Society of Sugar Beet Technologists
Avr	Avirulence
BaYMV	Barley yellow mosaic virus
<i>Bb</i>	Annuality (alleles)
BBSV	Beet black scorch virus
BCTV	Beet curly top virus
BdMoV	Burdock mottle virus
BMV	Beet mild yellowing virus
BNYVV	Beet necrotic yellow vein virus
BOLV	Beet oak leaf virus
BRLS	Benyvirus replicase-related sequence
BSBMV	Beet soil-borne mosaic virus
BSBV	Beet soil-borne virus
BSMV	Barley stripe mosaic virus
BVQ	Beet virus Q
°Bx	Brix (refractometer degree or optical density)
BWYV	Beet western yellows virus
BYV	Beet yellows virus
C	Cysteine
Cas9	CRISPR-associated protein 9
CAV	Chara australis virus
CC	Coiled-coil

CCC	Copyright Clearance Center (www.copyright.com)
cDNA	Complementary DNA
CdTe	Cadmium telluride
CEC	Cation exchange capacity
CHS	Chalcone synthase
CLS	Cercospora leaf spot
cM	Centimorgan
CMS	Cytoplasmic male sterility
CP	Coat protein or capsid protein
	Cross-protection test
	CP-mediated protection
CRA-CIN	Centro per la Ricerca in Agricoltura – Centro per le Colture Industriali
CRISPR	Clustered regularly interspaced short palindromic repeats
CRP	Cysteine-rich protein
CWR	Crop wild relatives
D	Aspartic acid
DAS-ELISA	Double-antibody sandwich enzyme-linked immunosorbent assay
DCL	Dicer-like
D-D	Mixture dichloropropene + dichloropropane
DI	Disease index
d _N	Non-synonymous substitution
DNA	Deoxyribonucleic acid
DPI	Days post inoculation
d _S	Synonymous substitution
dsRNA	Double-stranded RNA
dT	Deoxythymidine
E	Glutamic acid
E, N, Z	Production ability of sugar beet varieties
ed, eds	Editor, editors
EDTA	Ethylenediaminetetraacetic acid
eGFP	Enhanced green fluorescent protein
ELISA	Enzyme-linked immunosorbent assay
EPPO	European-Mediterranean Plant Protection Organization
ER	Endoplasmic reticulum
F	Phenylalanine
F-box	Cyclin F motif-containing protein
FLIM	Fluorescence lifetime imaging
FRET	Fluorescence resonance energy transfer
GFP	Green fluorescent protein
GM	Genetically modified
GMO	Genetically modified organism
GO	Argonaute

GORV	Gentian ovary ring-spot virus
Gp-1a, GP1b, GP-2, GP-3	Primary, secondary, and tertiary <i>Beta</i> gene pool
GSP	Gene-specific primer
GST	Glutathione S-transferase
H	Histidine
Hel	Helicase
HR	Hypersensitive response
HrpZ	Harpin Z
Ibid.	Published in the formerly cited paper
IBPGR	International Board Plant Genetic Resources
IIRB	International Institute of Sugar Beet Research
IMP	Immunodominant membrane protein
ISEM	Immunosorbent electron microscopy
ITS	Internal transcribed spacers
IWGPVVFV	International Working Group on Plant Viruses with Fungal Vectors
kDa	Kilodalton
kPa	Kilopascal
KWS	Kleinwanzlebener Saatzucht (seed company)
L	Leucine
LAI	Leaf area index
LSCS	Low sugar content syndrome
LSD	Least significant difference
MAPK	Mitogen-activated protein kinase
ML	Maximum likelihood
<i>Mm</i>	Monogermity (alleles)
mM	Millimoles
MP	Movement protein
MPN	Most probable number
mRFP	Monomeric red fluorescent protein
mRNA	Messenger RNA
MS	Male sterility
MT	Methyltransferase
N	Normal cytoplasm
NB-LRR	Nucleotide-binding site-leucine-rich repeat
NCR	Noncoding region
ncRNA	Noncoding RNA
NES	Nuclear exporting signal
NGS	Next-generation sequencing
NLS	Nuclear localization signal
NoLS	Nucleolar localization signal
nPCR	Nested PCR
nt	Nucleotides
NTPase	Nucleoside triphosphatase
NVMV	Nicotiana velutina mosaic virus

OA	Origin of assembly
ORF	Open reading frame
O-Type	CMS maintainer
p, pp	Page, pages
PCR	Polymerase chain reaction
PCV	Peanut clump virus
Pd	Plasmodesmata
PDR	Pathogen-derived resistance
pH	Acidity/basicity of aqueous solution
PMTV	Potato mop-top virus
ppm	Parts per million
PR	Pathogenesis-related
Pro	Protease
PspH	<i>Pseudomonas syringae</i> pv. <i>phaseolicola</i>
PTGS	Posttranscriptional gene silencing
PVX	Potato virus X
QD	Quantum dot
qPCR	Quantitative polymerase chain reaction
qRT-PCR	Quantitative reverse transcriptase polymerase chain reaction
QTL	Quantitative trait locus
RB	Resistance-breaking
RdDM	RNA-directed DNA methylation
rDNA	Ribosomal DNA
RdRp	RNA-dependent RNA polymerase
Rep0/3/5/III	Replicon 0, 3, 5 or III
RFLP	Restriction fragment length polymorphism
RISC	RNA-induced silencing complex
RNA	Ribonucleic acid
RNAi	RNA interference
ROS	Reactive oxygen specie
rpm	Revolutions per minute
rRNA	Ribosomal RNA
RS	Rizomania Signal (in German)
RSNV	Rice stripe necrosis virus
RT	Read-through
RTD	Read-through domain
RT-PCR	Reverse transcriptase polymerase chain reaction
Rz1; Rz2; Rz3; Rz4; Rz5	Resistances to rhizomania
<i>Rz1rz1; Rz2rz2; Rz3rz3</i> etc.	Alleles of rhizomania resistances
S	Sterile cytoplasm
°S	Polarization or sugar content (% w/w)
SBWMV	Soil-borne wheat mosaic virus
scFv	Single-chain antibody fragment
SDS	Sodium dodecyl sulfate

SES	Société Européenne des Semences (seed company)
siRNA	Small interfering RNA
SNP	Single-nucleotide polymorphism
SP	Signal peptide
sp.	Species (singular)
spp.	Species (plural)
SSCP	Single-strand conformation polymorphism
ssRNA	Single-stranded RNA
subsp.	Subspecies
T	Tyrosine
TA	Transcriptional activation
TAS-ELISA	Triple-antibody sandwich enzyme-linked immunosorbent assay
TEM	Transmission electron microscopy
TEV	Tobacco etch virus
TGB	Triple gene block
TIR	Toll/interleukin-1 receptor
TMV	Tobacco mosaic virus
TRV	Tobacco rattle virus
USDA	US Department of Agriculture
UTR	Untranslated region
V	Valine
VIGS	Virus-induced gene silencing
VLRA	Virus-like RNA assembly
VSR	Viral suppressor of RNA silencing
VY	Virus yellows
w/v	Weight unit of solute in volume units of solution
w/w	Weight units of solute in weight units of solution
WB	Wild beet
WSSMV	Wheat spindle streak mosaic virus
XRN	Exoribonuclease
XxZz	Male sterility (alleles)
μl	Microliters

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Part I
Historical Background

Chapter 1

Introduction

Enrico Biancardi and Robert T. Lewellen

Abstract The use of beets as a sugar-producing crop is rather recent, dating to a little over two centuries ago. However, domestication of beets dates back to prehistoric times. The history of the crop is summarized and represents an outstanding example of agricultural accomplishment. Sugar beet is subjected to a number of biotic and abiotic factors that more or less severely limit both sugar yield and processing quality. As it is for industrial purposes with specific requirements, sugar beet cultivation has been always more difficult than other crops. It is believed that agricultural innovation was introduced to accommodate cropping systems (e.g., crop rotation, row cropping) and technology to improve the sucrose production and its extraction (e.g., progeny testing). Among the diseases affecting the crop, rhizomania is certainly the most dangerous. Currently, the cropping of sugar beet would be difficult without the availability of some source of rhizomania resistance. The economic damage caused by rhizomania and its rapid spread across the world are described.

Keywords Sugar beet • Rhizomania • BNYVV • *Polymyxa betae* • Genetic resistances

Farming sugar beet began in Germany just over two centuries ago. Within a few decades, the crop assumed increasing importance in a number of European countries. Despite higher cultivation costs and care needed to grow a successful crop, farmer's income was improved by including sugar beet in the rotation. Moreover, the industry was based, often for the first time, in the countryside and every sugar factory provided employment for hundreds of workers. The crop rapidly became a hub of the economy and technical evolution of agriculture. Intended to counteract the monopoly of sugar produced by cane, sugar beet had to survive times of trouble (social, economic, political) due not only to the frequent world overproduction and consequent low prices, but also to the spread of serious diseases. Rhizomania has been one of these for around half a century, becoming rapidly widespread all over

E. Biancardi (✉)

Formerly: Stazione Sperimentale di Bieticoltura, Rovigo, Italy

e-mail: enrico.biancardi@alice.it

R.T. Lewellen

Formerly: USDA-Agricultural Research Service, Salinas, CA, USA

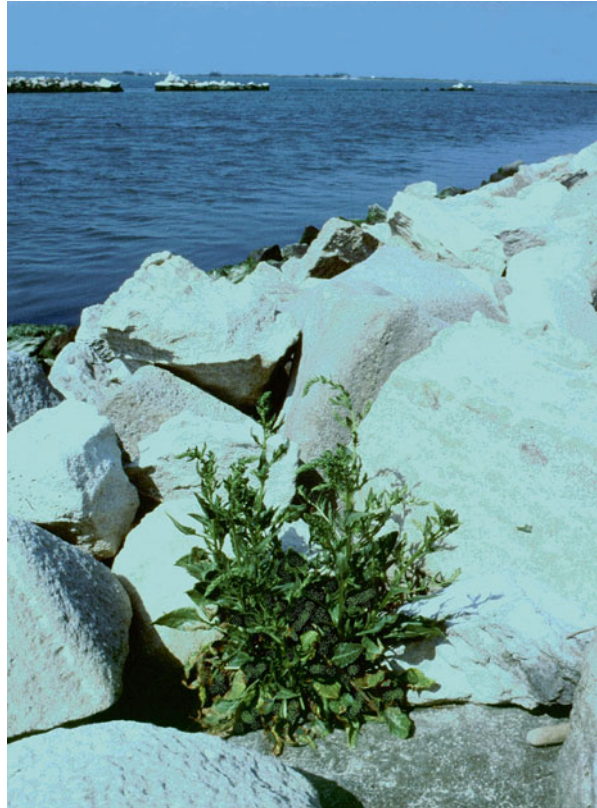
e-mail: rtlewellen@hotmail.com

the world with rare exceptions. So far, breeding research has allowed satisfactory control of the damages by means of resistant varieties. Despite this, the disease is still rapidly expanding.

1.1 Beets and Sugar Beets

The wild ancestor was similar to the current sea beet [*Beta vulgaris* L. subsp. *maritima* (L.) Arcang.] (Fig. 1.1), now classified as a subspecies (subsp.) together with different types of cultivated beets, *Beta vulgaris* (*Beta vulgaris* L. subsp. *vulgaris*) (Ford-Lloyd et al. 1975; Ford-Lloyd 2005). The subspecies *vulgaris* and *maritima* belong to the species *vulgaris*, included in the section *Beta* (*Vulgares*), genus *Beta*, and family Amaranthaceae (formerly Chenopodiaceae). The other species and subspecies of the genus *Beta* (Box 1.1), usually named “wild beets,” do not have commercial value. However, with the expected progress in molecular biology and gene transfer, they could become future sources of traits useful for the cultivated varieties. As crosses with wild beets of other sections of the genus *Beta* are difficult using traditional means, the best results so far have been obtained with *B. maritima*.

Fig. 1.1 *Beta maritima* living in very difficult conditions near Porto Levante, Italy. From beets collected at the same site in 1909, resistances to cercospora leaf spot and rhizomania have been obtained (Biancardi et al. 2012)



Box 1.1: Taxonomy of Genus *Beta*

Based on molecular phylogenetics, a modified taxonomy of the genus *Beta* was proposed by Kadereit et al. (2006) and Hohmann et al. (2006). More recently, Kadereit et al. (2006) suggested the reintroduction of the subfamily *Betoideae*, first proposed by Ulbrich (1934), because it better explains the position of the genus *Beta* inside the family or “alliance” Chenopodiaceae/Amaranthaceae and fits better with the analysis of the nuclear ribosomal ITS1 sequences. According to this proposal, the taxonomy of the genus *Beta* was revised by moving the section IV *Procumbentes* into another genus due to the differences between it and the species in the section I *Beta*. To do this, Kadereit et al. (2006) proposed the introduction of a separate genus *Patellifolia*, including the species *procumbens*, *patellaris*, and *webbiana* (Table 1.1). They also suggested the elimination of the section III *Nanae*, incorporating *Beta nana* (the lone species in that section) into section *Corollinae*. Hohmann et al. (2006), according to Kadereit et al. (2006), included only two sections (*Beta* and *Corollinae*) in the genus *Beta*. The family Amaranthaceae belongs to the order *Caryophyllales* (McGrath and Townsend 2015).

Table 1.1 Comparison of the taxonomy of the genus *Beta* proposed by Ford-Lloyd (2005) and Kadereit et al. (2006)

Ford-Lloyd (2005)	Kadereit et al. (2006)
Genus <i>Beta</i>	Genus <i>Beta</i>
Section I <i>Beta</i> (<i>Vulgares</i>)	Section I <i>Beta</i>
<i>Beta vulgaris</i>	<i>Beta vulgaris</i>
subsp. <i>vulgaris</i> (cultivated forms ^a)	subsp. <i>vulgaris</i> (cultivated forms ^a)
subsp. <i>maritima</i>	subsp. <i>maritima</i>
subsp. <i>adanensis</i>	subsp. <i>adanensis</i>
<i>Beta macrocarpa</i>	<i>Beta macrocarpa</i>
<i>Beta patula</i>	
Section II <i>Corollinae</i>	Section II <i>Corollinae</i>
<i>Beta corolliflora</i>	<i>Beta corolliflora</i>
<i>Beta lomatogona</i>	<i>Beta lomatogona</i>
<i>Beta intermedia</i>	<i>Beta trigyna</i>
<i>Beta trigyna</i>	<i>Beta nana</i>
Section III <i>Nanae</i>	
<i>Beta nana</i>	
Section IV <i>Procumbentes</i>	Genus <i>Patellifolia</i>
<i>Beta procumbens</i>	<i>Patellifolia procumbens</i>
<i>Beta patellaris</i>	<i>Patellifolia patellaris</i>
<i>Beta webbiana</i>	<i>Patellifolia webbiana</i>

^aCultivated forms include sugar beet group, leaf beet group, fodder beet group, and garden beet group (Lange et al. 1999)