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T G R C

Tomato Genetics Resource Center

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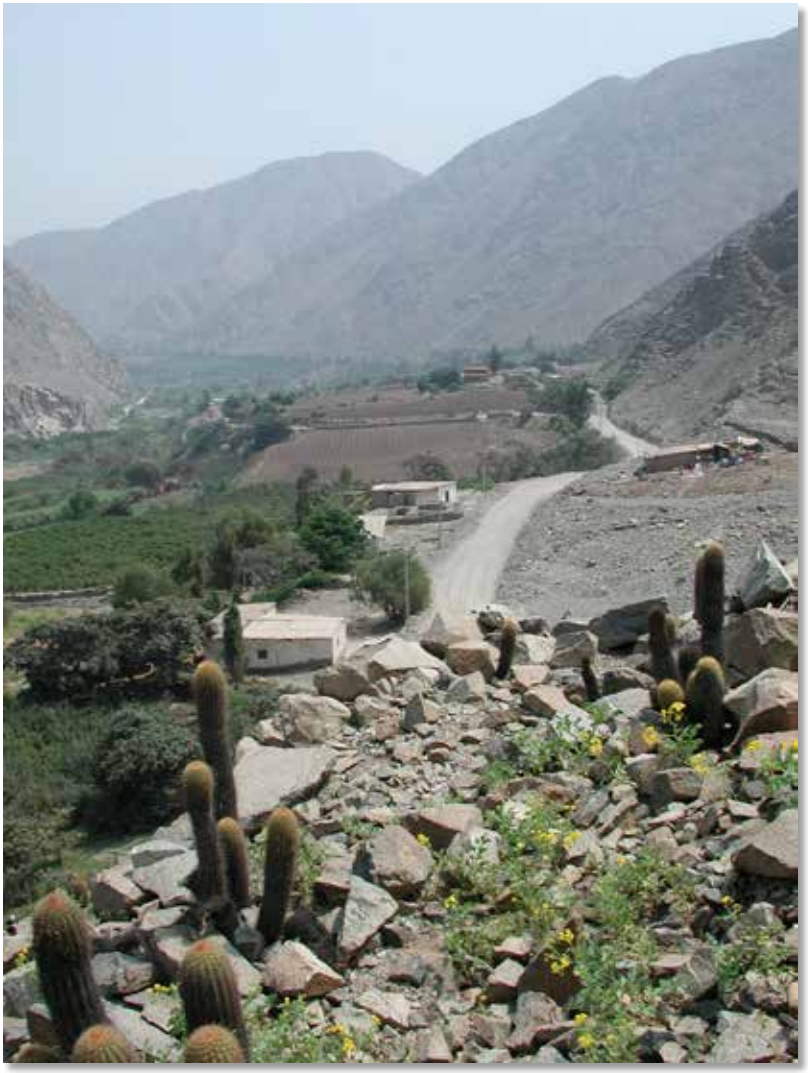
ANNUAL PROGRESS REPORT

2017



Plants of *Solanum pennellii* growing near Sisacaya, Peru. The wild tomato *S. pennellii* has been widely used by researchers and breeders as a source of novel traits not found in cultivated tomato. Hybrids with cultivated tomato are easily obtained when the wild species is used as the pollen parent. In the reciprocal cross, pollen of cultivated tomato is rejected on pistils of *S. pennellii* by unilateral incompatibility. Research led by the TGRC has identified a major gene, *FPS2,* that determines pollen compatibility. The work by Qin *et al.* 2018 in *The Plant Journal* highlights a previously unknown mechanism of pollen rejection. [photo Roger Chetelat, 2009]

The TGRC thanks the following organizations for providing financial support in 2017.

SUMMARY

Acquisitions. The TGRC acquired 444 new accessions this year, including a large set of backcross inbred lines (BILs) from *S. pennellii* LA0716 in cv. M82, as well as an accession of *S. pennellii* used for genome sequencing, and an introgression line with a segment of *S. lycopersicoides* chromosome 12. Obsolete or redundant accessions were dropped. The current total of number of accessions maintained by the TGRC is 4,360.

Maintenance and Evaluation. A total of 1,576 cultures were grown for various purposes, of which 974 were for seed increase, including 53 wild species accessions. Germination tests were run on 655 seed lots. Progeny tests were performed on 89 stocks of male-steriles, trisomics, and other segregating lines or accessions with unexpected phenotypes. 175 stocks were grown for introgression of the *S. sitiens* genome. Other stocks were grown for research on interspecific reproductive barriers. All plants grown for seed regeneration were tested twice for PSTVd; no positive plants were found. Newly regenerated seed lots were split, with one sample stored at 5° C to use for filling seed requests, the other stored in sealed pouches at -18° C to better maintain long term seed viability. For backup storage, 93 seed samples were sent to the USDA and 26 samples were sent to the Svalbard Global Seed Vault.

Distribution and Utilization. A total of 5,978 seed samples representing 2,241 different accessions were distributed in response to 330 requests from 275 researchers and breeders in 31 countries; at least 17 purely informational requests were also answered. The overall utilization rate (i.e. the number of samples distributed relative to the number of accessions available) was 137%. Information provided by recipients indicates our stocks continue to be used to support a wide variety of research and breeding projects. Our annual literature search uncovered 115 publications that mention use of our stocks.

Documentation. On our website we added a 'comments' page to facilitate user feedback, and we removed most contact information on users to protect their privacy. Additional images of mutants and wild species were uploaded. Passport data on new accessions was added. Seed request records and passport information on seed samples submitted for off-site back up were provided to the USDA for uploading to their GRIN-Global database.

Research. The TGRC continued research on the mechanisms of interspecific reproductive barriers and on introgression of the *S. sitiens* genome. We published a paper on natural variation for pollen incompatibility genes in *S. arcanum, S. chmielewskii*, and *S. neorickii.* We further advanced a set of breeding lines representing the genome of *S. sitiens* in a cultivated tomato background. The goal of this project is to develop a set of 'introgression lines' – prebred stocks containing defined chromosome segments from the donor genome – that will provide the first breeder friendly germplasm resources for this wild species. We contributed to a paper reporting a second reference genome sequence for *S. pennellii*. We also participated in collaborative research to evaluate methods for creating doubled haploids by manipulation of centromere histone proteins.

ACQUISITIONS

The TGRC acquired 444 new accessions in 2017. Dr. Dani Zamir at the Hebrew University of Jerusalem, Rehovot campus, donated a set of 442 backcross inbred lines (BILs) representing the genome of *S. pennellii* LA0716 in the background of cv. M82 (Ofner *et al.* 2016 *Plant Journal* 87: 151-160). Each BIL has from one to several introgressed *S. pennellii* chromosome segments. The end points of each introgression have been precisely determined by DNA analysis using SNPs (Single Nucleotide Polymorphisms). Compared to introgression lines,

the BILs are more informative for mapping traits and for studying interactions between two or more loci affecting the same trait but located on different chromosomes (Fulop *et al.* 2016 *G3-Genes, Genomes, Genetics* 6:3169-3184). The BILs were grown in the field or greenhouse in 2017 and displayed wide variation in morphology.

Dr. Zamir also donated a stock of *S. pennellii*, LA5240, which has proved to be useful in his research because it is self-compatible and has a more vigorous, disease resistant root system than LA0716, another self-compatible biotype. This stock of *S. pennellii* is of unknown origin, and was discovered by Dr. Zamir in a seed sample received from the IPK genebank in Gatersleben, Germany. LA5240 has been used recently to generate a high quality reference genome sequence using the Oxford Nanopores technology (Schmidt *et al.* 2017 *The Plant Cell* 29: 2336-2348). Finally, the TGRC selected an introgression subline, LA4312B, representing part of chromosome 12 from *S. lycopersicoides* in the background of cv. VF 36.

Inflorescence of *S. pennellii* LA5240.

More detailed information on the recently acquired accessions can be found on our website at http://tgrc.ucdavis.edu/acq.aspx. Obsolete or redundant accessions were dropped. The current total of number of accessions maintained by the TGRC is 4,360.

Table 1. Number of accessions of each species maintained by the TGRC. The figures include accessions that are temporarily unavailable for distribution.

***Solanum* spp.**	***Lycopersicon* equivalent**	**# Accessions**
S. lycopersicum	*L. esculentum*, including var. *cerasiforme*	3,221
S. pimpinellifolium	*L. pimpinellifolium*	334
S. cheesmaniae	*L. cheesmanii*	42
S. galapagense	*L. cheesmanii* f. *minor*	29
S. chmielewskii	*L. chmielewskii*	16
S. neorickii	*L. parviflorum*	47
S. arcanum	*L. peruvianum*, including f. *humifusum*	45
S. peruvianum	*L. peruvianum*	70
S. huaylasense	*L. peruvianum*	16
S. corneliomulleri	*L. peruvianum*, including f. *glandulosum*	53
S. chilense	*L. chilense*	112
S. habrochaites	*L. hirsutum,* including f. *glabratum*	123
S. pennellii	*L. pennellii*, including var. *puberulum*	47
S. lycopersicoides	n/a	23
S. sitiens	n/a	13
S. juglandifolium	n/a	5
S. ochranthum	n/a	7
Other (interspecific hybrids, RILs)	n/a	150
Total		**4,360**

MAINTENANCE

Scott Peacock and his crew of undergraduate student assistants performed a large number of field and greenhouse plantings this year. A total of 1,576 families were grown for various purposes; 974 of these were for seed increase, including 53 of wild species accessions, most of which required greenhouse culture; 175 were for introgression and analysis of the *S. sitiens* genome. The rest were grown for germination tests (655), progeny tests (89), tests of PSTVd transmission (30), or other purposes.

Identifying accessions in need of regeneration begins with seed germination testing. We test all seed lots after 10 years of storage. Seed samples that do not meet our threshold of 80% germination after two weeks are normally regenerated in the same year. Seed lots that meet the threshold are retested again in two years. Other factors, such as available greenhouse space, age of seed and supply on hand, are also taken into account. Newly acquired accessions are typically regenerated in the first year or so after acquisition because seed supplies are limited and of uncertain viability. This year, 655 seed lots from 2007 or earlier were tested for germination rates. Average germination values continued to be relatively high for most species (Table 2), however we obtained relatively low germination rates from some seed samples of cultivated tomato and *S. chilense,* as well as the four tomato-like nightshade species.

Table 2. Results of seed germination tests. Values are based on samples of 25-50 seeds per accession, and represent the % germination after 14 days at 25°C. Seed lots with a low germination rate are defined as those with less than 80% germination.

***Solanum* Species**	**Date of Tested Lots**	**# Tested**	**Avg % Germ**	**# Low Germ**	**# Grown[1]**
S. lycopersicum	2003-2007	384	73.8	112	814
S. pimpinellifolium	2000-2007	42	93.4	5	15
S. cheesmaniae, S. galapagense	2003-2008	27	93.9	2	6
S. chmielewskii, S. neorickii	2005-2007	12	96.3	1	1
S. chilense	1990-2007	44	75.5	18	4
S. peruvianum, S. arcanum, S. corneliomulleri, S. huaylasense	2003-2007	66	89.1	9	4
S. habrochaites	1982-2007	54	96.0	2	4
S. pennellii	2003-2007	10	95.2	0	1
S. lycopersicoides	2001-2007	7	66.0	5	1
S. sitiens	2002-2006	6	59.3	6	1
S. juglandifolium	2006-2007	2	27.0	2	2
S. ochranthum	2005	1	88.0	0	0
Total		**655**	**79.8**	**168**	**853**

[1]Includes accessions regenerated for reasons other than low germination (e.g. newly acquired, low supply, etc).

We again planted a relatively large number of cultivated tomato and *S. pimpinellifolium* genotypes in the field this year, occupying a total of 69 rows. The usual sequential plantings were made to spread the workload. Seedlings were transplanted into the field on four separate dates, the first of which was May 4th. Early growth and establishment were satisfactory, however daytime high temperatures were unfavorable for fruit set for extended periods of time in July and August. Some lines such as the BILs and some primitive cultivars from Ecuador and Peru did not yield large amounts of seed may need to be regrown next year. We again used drip irrigation this year, and improved seedling establishment over last year by wetting the soil profile

more thoroughly prior to transplanting. Cutting off the drip irrigation late in the season helped prevent excessive growth of the indeterminate lines.

Backcross inbred lines (BILs) of *S. pennellii* in cv. M-82.

Most of the wild species, many mutants and certain other genetic stocks require greenhouse culture, either for isolation purposes or because they do not grow or flower well under field conditions. For the mutant stocks, we sow the weakest lines first, and finish with lines of normal vigor. Our schedule of greenhouse plantings of the wild species is based on photoperiod responses: those with the least sensitivity are planted first, in the early spring; those with intermediate reaction are planted in early summer; the most sensitive (i.e. flower best under short days) are planted in mid-summer for fall blooming. Optimal planting dates and other growing recommendations for each species are listed on our website.

Preventing the spread of seed borne pathogens is an important aspect of any seed regeneration program. We inspect all our plantings throughout the growing cycle for disease symptoms. Plants displaying signs of disease are tested with Agdia ImmunoStrips. This year TSWV was less of a problem in our field and greenhouse plantings than in previous years. All stocks were tested for the presence of PSTVd, both the seedling stage and at mature plant stages, and all results were negative. As a precaution, we continue to treat all seed lots used for distribution with dilute acid (1% HCl for 5 mins) and bleach (1% hypochlorite for 5 mins) to prevent transmission of seed borne pathogens.

Samples of all newly regenerated seed lots were catalogued then stored at 5°C – our working collection, used for filling seed requests -- and at -18°C for long term preservation of viability. We continue to use Zeolite beads to dry seed to ultralow moisture levels prior to sealing in foil pouches, then stored at -18°C or 5°C. Our current -18°C seed storage units are at capacity; we hope to build a walk-in -18C seed vault when sufficient funding is secured. As in the past, large samples of newly regenerated seed lots were sent to the USDA National Laboratory for Genetic Resources Preservation in Ft. Collins, Colorado, and the Svalbard Global Seed Vault in Norway for long-term backup storage. This year 93 accessions were sent to NLGRP and 26 to Svalbard.

EVALUATION

All stocks grown for seed increase or other purposes were systematically checked to ensure that they have the correct phenotypes. New accessions were evaluated in greater detail, with the descriptors depending upon type of accession (wild species, cultivar, mutant, chromosomal stocks, etc.). Plantings were reviewed at different growth stages to observe foliage, habit, flower morphology, fruit set, and fruit morphology. Images of selected accessions were uploaded to our website.

Many genetic stocks, including various sterilities, nutritional, and weak mutants, cannot be maintained in true-breeding condition, hence have to be transmitted from heterozygotes. Progeny tests must therefore be made to verify that individual seed lots segregate for the gene in question. Other accessions may show unexpected segregation or off-types due to outcrossing, and need to be progeny tested to reestablish true breeding lines. We sowed 89 lines for progeny testing of male-steriles or other segregating mutants, as well as various other stocks with incorrect phenotypes. This year's progeny tests included stocks of the following mutant loci: *suppressor of self-pruning, single flower truss, terminal flower-2, male-sterile-10, -15, -31,* and *-32, bushy, Delta, pistillate-2,* and *midget.* In addition, we grew progeny tests of a dwarf mimic, introgression lines, accessions of *S. pennellii* and *S. chilense*, and primitive cultivars that showed unexpected segregation or off-types, or for identification purposes.

DISTRIBUTION AND UTILIZATION

A total of 5978 seed packets of 2241 different accessions were sent in response to 330 seed requests from 275 scientists, breeders and educators in 31 countries. About 18% of the samples went to users in the private sector, and 82% were sent to public sector researchers. Relative to the size of the TGRC collection (4360 accessions), the number of seed samples distributed (5978) was equivalent to a utilization rate of 137%. Over half of our 4360 accessions were requested at least once in 2017, confirming that we maintain relatively few 'obsolete' stocks. At least 17 purely informational requests were answered.

The various steps involved in filling seed requests – selecting accessions, treating and repackaging seeds, entering the information into our database, providing cultural recommendations, obtaining phytosanitary certificates and import permits, etc. – involve a large time commitment. The TGRC crew has worked diligently to fill seed requests while implementing stringent phytosanitary practices. We continue to use an online payment system to recover the costs of phytosanitary certificates and express mail shipping. Finding the most reliable shipping method for each country takes time. Shipments are sometimes delayed or lost and need to be refilled.

Information provided by recipients regarding intended uses of our stocks is summarized in Table 3. As in previous years, there was a notable emphasis on disease insect pest resistance, both for breeding purposes and for research. The diseases generating the most requests were TYLCV, TSWV, and bacterial canker. There continues to be strong interest in abiotic stress responses, particularly drought and high/low temperature extremes. There were many requests for research on evolutionary aspects, including diversity and genome-wide association studies (GWAS). There was much interest in grafting, graft transmissibility, and rootstock breeding. Studies of various reproductive traits, including crossing barriers, flower morphology and volatiles, were mentioned in a large number of requests. There were also a large number of requests for studies of trichomes and for wounding/defense responses. We again received a significant number of requests for instructional uses. As in the past, the largest numbers of requests mentioned only 'breeding' or 'research'.

We continue to receive more and more requests for introgression lines (ILs), nearly isogenic lines (NILs), and other prebreds. A total of 35 requests and 518 seed samples were processed for the *S. pennellii* ILs, 18 requests and 297 samples for the *S. habrochaites* ILs, and 27 requests and 334 samples for the *S. lycopersicoides* ILs. We also sent out 265 samples of *S. lycopersicum* x *S. pimpinellifolium* recombinant inbred lines in response to 13 requests. These numbers show that breeders and researchers continue to find many uses for prebred germplasm.

Table 3. Intended uses of TGRC stocks as reported by requestors. Values represent the total number of requests mentioning each keyword or category. Requests addressing multiple topics may be counted more than once.

Category	#
Biotic Stresses	
Viruses:	
PepMV	1
ToMV	1
TSWV	3
TYLCV	4
Viroids	1
Unspecified viruses	3
Bacteria:	
Bacterial canker	3
Bacterial speck	1
Bacterial wilt	2
Salmonella	1
Other bacteria	2
Fungi:	
Cladosporium	2
Corky root	1
Fusarium spp.	1
Phytophthora spp.	2
Powdery mildew	1
Septoria	1
Verticillium	1
Target spot	2
Other fungi	5
Nematodes	6
Unspecified diseases	29
Insect pests	10
Parasitic plants	4
Abiotic Stresses	
Acid soils	1
Drought	11
High temperatures	8
Low temperatures	5
Salinity	4
Unspecified abiotic	8
Fruit Traits	
Alkaloids	
Anthocyanins	3
Carotenoids	3
Flavor, volatiles	4
Fruit devel./ripening	3
Parthenocarpy	
Quality	2
Shelf life	1
Yield	3
Other fruit traits	3
Breeding	
Grafting, rootstocks	7
Introgression	1
Male steriles, allogamy	2
Marker development	1
Prebreeding	2
Unspecified breeding	22
Genetic Studies	
CRISPR/Cas9	2
Epigenomics	1
Evolution, diversity	7
Functional genomics	1
Genomics	1
Gene cloning	1
Gene expression, regul.	6
GWAS	2
Mapping, QTLs	3
Segregation distortion	1
siRNAs	3
Transformation	2
Transposable elements	1
Other genetic studies	3
Physiology & Develop.	
Carbohydrate metabol.	1
Flower morph/develop	4
Hormone responses	5
Innate immunity	1
Leaf develop./shape	5
Metabolites	6
Microbiomes	1
Nutrient uptake	4
Photosynthesis, respire.	2
Phenotyping	2
Reproductive biology	4
Root growth/develop.	2
Sesquiterpenes	1
Stomatal responses	2
Trichomes	10
Volatiles	2
Wounding, defense	8
Other physiol/develop	4
Miscellaneous	
Instructional uses	6
Unspecified research	52

Our survey of the 2017 literature and unreviewed papers of previous years uncovered 115 journal articles, reports, abstracts, theses, and patents that mention use of TGRC stocks (see Bibliography, below). Many additional publications were undoubtedly missed, and cases of utilization by the private sector are generally not publicized. These publications, many in high impact journals, show that TGRC germplasm continues to be employed for a wide range of basic and applied research, breeding and educational purposes.

DOCUMENTATION

Our database was modified in various ways by Tom Starbuck to improve internal record keeping, fix bugs, and add functionality to our tables, forms, and queries. Additional images of mutants and wild species accessions were uploaded and are accessible on our website. Passport data on new accessions was added and records on existing accessions were updated as needed to

correct errors or incorporate new information. On our website, Tom added a page for user feedback and disabled display of most contact information on users due to privacy considerations. As in the past, we provided the USDA National Plant Germplasm System with passport data on accessions sent to them for back up storage for uploading into their GRIN-Global database. Seed distribution records and summary statistics were also provided to the USDA.

RESEARCH

The TGRC is pursuing several research projects related to genetic resources and breeding barriers. One project, supported from the National Science Foundation, aims to decipher the genetic mechanisms of pollen/pistil incompatibility in wide crosses of tomato. Dr. Xiaoqiong Qin identified and studied a gene, *FPS2,* that is required for pollen to avoid rejection on pistils of the wild species *S. pennellii*. She showed the *FPS2* is part of a previously unknown mechanism for rejecting foreign pollen. Unlike previously identified pollen incompatibility factors, *FPS2* act independently of self-incompatibility, a mechanism that regulates pollen recognition in some wild relatives of tomato. Dr. Mira Markova studied natural variation for two self-incompatibility factors, *Cullin1* and *SLF-23*, in three closely related wild tomato species: *S. arcanum* (self-incompatible), *S. chmielewskii* (self-compatible), and *S. neorickii* (self-compatible). Her results show that self-compatibility evolved at least twice and via independent genetic mutations. Her findings were published in the *American Journal of Botany* this year.

A *S. sitiens* introgression line with parthenocarpic (seedless) fruit that ripen unevenly. [photo Scott Peacock]

Another research project, funded by the USDA-NIFA's Plant Breeding program, seeks to develop a set of introgression lines representing the genome of *S. sitiens*. This wild tomato relative is known for its tolerance to drought, salinity, and low temperatures, as well as unique fruit traits and disease resistance. However strong breeding barriers have prevented crosses with tomato until recently. Introgression lines (ILs) are prebred stocks containing defined chromosomal segments from the wild species' genome in the genetic background of cultivated tomato. The goal is to create a library of 50-100 ILs that capture the *S. sitiens* genome in a uniform, cultivated tomato genetic background. Dr. Xiaoqiong Qin and Meilian Tan further advanced each line by backcrossing and marker assisted selection using DNA markers, and produced homozygous (stable) versions of each line wherever possible. In the coming year the lines will be genotyped to high reso lution using SNPs and we will begin evaluating them for certain economic traits of interest.

PUBLICATIONS

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SERVICE AND OUTREACH

Presentations. Presentations on the TGRC, research projects, and related topics were given to: the 'TRADITOM' project review meeting in Tenerife (Spain), the UC Davis Integrated Genetics and Genomics graduate group seminar, the 'EU-SOL' project review meeting in Turin (Italy), the IPK in Gatersleben (Germany), the University of Valencia (Spain), the Hebrew University of Jerusalem (Israel), Michigan State University, the annual meeting of the California Tomato Research Institute, the Bayer Crop Science in West Sacramento, and students from Esparto High School. A guest lecture was presented in a course on "Plant Conservation Genetics" at UC Davis.

Press Coverage. RTC was interviewed for a journalism student's project on the politics of funding for research on tomato genetics.

Visitors. The TGRC provided presentations and tours to visitors from East West Seeds, Rijk Zwaan Breeding, Nippon Del Monte, Tarbiat Modares University (Iran), University of Tsukuba (Japan), HM Clause, Ankur Seeds, Plenty, UC Davis College of Agricultural and Environmental Sciences Dean's Office, UC Davis Dept. of Plant Sciences, Monsanto, Olam, UC Cooperative Extension, KraftHeinz, The Morning Star Company, Sakata Seeds America, Cochran Fellows from Kenya and Uganda, Kyungpook National University (South Korea), and the European Plant Breeding Academy.

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PERSONNEL

Scott Peacock continues to run our seed regeneration and testing program. Adryanna Corral, previously in charge of seed distribution, left for graduate school and was replaced by Anastasia Mathews. Tom Starbuck, our long time database guru and webmaster, officially retired but has been recalled for one more year. Undergraduate student assistants Sarah Yam, Dragomira Zheleva, Ryan Hodge, Richie Ruiz and Magdalena Mendoza all graduated. Magdalena is still working for us on a short term appointment. Newly hired undergraduate students are Anastasia, Kyle Johnson, and Emily Schoenborn. In the lab, Dr. Xiaoqiong Qin switched projects, from reproductive barriers to *S. sitiens* introgression, and oversaw a student internship project by Oliver Betz. Post-doc Dr. Mira Markova and visiting scientist Dr. Meilian Tan, both left the lab and returned to their countries.

TESTIMONIALS

Thank you for kind guidance for importing accessions -Dr. P. Muthukumar

Thank you for your time and for providing this valuable resource. – Anna Klimes

Thank you for this great service to this tomato research community! TGRC has been a fundamental component of tomato and plant research. – Vagner Benedito

Thank you very much for everything, especially wild tomatoes. – Toshihito Tabuchi

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