Unraveling the history of selection in wild and cultivated chickpea

Peter Chang

Chickpea Innovation Lab Annual Meeting
Hyderabad, India

December 2017
Main Topics

• When was chickpea domesticated?
• How many times has domestication occur?
• What parts of the genomes have been selected?
• What are the mechanism for which selection has occurred?
Domestication: 10-12,000 years ago
Domestication: 10-12,000 years ago
Secondary diversification: ~6,000 years ago
Domestication: 10-12,000 years ago

Secondary diversification: ~3-4,000 years ago

Secondary diversification: ~6,000 years ago

Secondary diversification: ~3-4,000 years ago
Domestication: 10-12,000 years ago
Secondary diversification: ~3-4,000 years ago
Secondary diversification: ~3-4,000 years ago
Secondary diversification: ~6,000 years ago
Recent introduction: Within last century
Developing climate-resilient chickpea

- Chickpea improvement limited by low genetic diversity within the cultivated gene pool.
- Wild species hold promise for chickpea improvement

Cultivated Material have very low Genetic Diversity
Sampled 24 sites across the accessible range

<table>
<thead>
<tr>
<th>City/Province</th>
<th>Site/Location</th>
<th>Lat</th>
<th>Long</th>
<th>Elev</th>
<th>Location</th>
<th>ID from Seed Pictures</th>
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<tbody>
<tr>
<td>Adiyaman</td>
<td>Oyali/Besni/Adiyaman</td>
<td>37.7337</td>
<td>37.8030</td>
<td>931.27</td>
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<td>Cermik/Diyarbakir</td>
<td>38.0537</td>
<td>39.4219</td>
<td>774.16</td>
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<td>Egil/Diyarbakir</td>
<td>38.2744</td>
<td>40.0647</td>
<td>986.49</td>
<td>Egil</td>
<td>15 ret 1 pinnafidium</td>
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<td>38.0113</td>
<td>39.3747</td>
<td>839.56</td>
<td>Gunasan</td>
<td>5 ech-ret</td>
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<tr>
<td>Diyarbakir</td>
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<td>40.0854</td>
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<td>38.2039</td>
<td>39.6067</td>
<td>883.41</td>
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<td>40.8549</td>
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<td>Besevler</td>
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<td>Dargecit</td>
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<td>40.9077</td>
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<td>Savur</td>
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<td>37.4254</td>
<td>42.5027</td>
<td>1365.43</td>
<td>Cudi</td>
<td>17 reticulatum 2 bijugum</td>
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<td>15 reticulatum 2 bijugum</td>
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<td>Sarikaya/Midyat</td>
<td>37.5465</td>
<td>40.9077</td>
<td>1174.56</td>
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<td>all 4 reticulatum</td>
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<td>37.5467</td>
<td>42.5027</td>
<td>1365.43</td>
<td>Cudi</td>
<td>17 reticulatum 2 bijugum</td>
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<tr>
<td>Sirnak</td>
<td>Siv-Diyar road 130km from Urfa</td>
<td>37.8212</td>
<td>39.6417</td>
<td>1115.82</td>
<td>Siv-Diyar</td>
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<tr>
<td>Urfa</td>
<td>Destek</td>
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<td>39.1730</td>
<td>740.06</td>
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<tr>
<td>Urfa</td>
<td>Guvenli</td>
<td>37.7418</td>
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<td>Guvenli</td>
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<tr>
<td>Urfa</td>
<td>Karabahce</td>
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<tr>
<td>Urfa</td>
<td>Ortanca</td>
<td>37.4734</td>
<td>39.5632</td>
<td>861.04</td>
<td>Ortanca</td>
<td>all 11 echinospermum</td>
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</tbody>
</table>
24 Wild Turkey Field Sites

Cicer reticulatum as 8 Groups
24 Wild Turkey Field Sites

Cicer reticulatum as 8 Groups
24 Wild Turkey Field Sites

Cicer echinospermum as 4 Groups

Cicer reticulatum as 8 Groups

Ortanca
Guvenli
Kesentas
Cermik
Gunasan
S2Drd
Karabache
Kalkan
Egil
Sirnak
Savur
Kayatape
Dereici
Sarikaya
Dargecit
Kilavuz
Cudi A B
Besevler
Baristepe 1, 2, 3
Thal desert

Pothohar region
Accessing novel variation: Older Landraces

Collections by time

- 1911 - 1925
- 1926 - 1940
- 1941 - 1955
- 1956 - 1970
- 1971 - 1985
- 1986 - 2000
1000 Wild Cicer Accessions

Cicer echinospermum as 4 Groups

Cicer reticulatum as 8 Groups

1000 Cultivated Cicer Accessions

Cicer arietinum as 5 Groups

Turkish Landraces  |  PK  |  Ethiopia Landraces

Modern Breeding Chickpea Genotypes
$\Theta_w$ Watterson’s Estimator of Diversity

Increasing Diversity $\rightarrow$
$\Theta_w$ Watterson’s Estimator of Diversity

- 568 Ethiopian samples
- 147 Turkish samples
- 80 Indian/Pakistani samples

Increasing Diversity $\rightarrow$
$\Theta_w$ Watterson’s Estimator of Diversity

Increasing Diversity $\rightarrow$

- 568 Ethiopian samples
- 147 Turkish samples
- 80 Indian/Pakistani samples
- 54 Turkish LR samples
- 51 VIR-Turkish LR samples
- 47 VIR-Ethiopian LR samples
- 61 Ethiopian LR samples
- 57 Pakistani samples
- arietinum
- echinospermum
- reticulatum
G-PhoCS – Bayesian Analysis

$\theta = 4\mu N_e$, measure of diversity
$\mu = 10^{-8}$ mutation rate
$N_e$ is effective population size

$\theta = 9.0 \times 10^{-3}$
$\theta = 8.3 \times 10^{-5}$
$\theta = 1.1 \times 10^{-2}$

$\theta = 0.0090$ (100X Cult.)
$\theta = 0.011$ (100X Cult.)
$\theta = 0.00008$
G-PhoCS – Bayesian Analysis

$\theta = 4\mu N_e$, measure of diversity
$\mu = 10^{-8}$ mutation rate
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$\theta = 1.1 \times 10^{-2}$

$\theta = 8.3 \times 10^{-5}$

$\theta = 9.0 \times 10^{-3}$

$\theta = 0.0090 \ (100X \ Cult.)$

$\theta = 0.011 \ (100X \ Cult.)$

$\theta = 0.00008$

$\theta = 1.1 \times 10^{-2}$

$\theta = 1.4 \times 10^{-4}$

$\sim 2X \ Cult.$

$\theta = 4\mu N_e$, measure of diversity
$\mu = 10^{-8}$ mutation rate
$N_e$ is effective population size
G-PhoCS – Bayesian Analysis

\[ \theta = 4\mu N_e, \text{ measure of diversity} \]
\[ \mu = 10^{-8} \text{ mutation rate} \]
\[ N_e \text{ is effective population size} \]

\[ \begin{align*}
\theta &= 9.0 \times 10^{-3} \\
\theta &= 1.1 \times 10^{-2} \\
\theta &= 0.00008 \\
\end{align*} \]

95-127 KYA

\[ \theta = 1.1 \times 10^{-3} \text{ (10X Cult.)} \]

9-12 KYA

\[ \theta = 1.4 \times 10^{-4} \text{ ~2X Cult.} \]

Present

\[ \theta = 0.0090 \text{ (100X Cult.)} \]
\[ \theta = 0.011 \text{ (100X Cult.)} \]
\[ \theta = 0.00008 \]

Ce Cr Ca - cultivated
Wild and Cultivated Donors

Cermi_075, Bari1_092, Derei_072, Dikbas
Deste_080, Bari2_072N2, Egill_065, Gocke
Gunas_062, Bari3_072C, Egill_073, Habru
Karab_092, Bari3_100, Kalka_064, ICCV2
Ortan_066, Bari3_106D, Kayat_077, ICCV96029
S2Drd_065, Besev_075, Kesen_075, Minjar
Besev_079, Oyali_084
CudiA_152, Sarik_067
CudiB_022C, Savur_063
Derei_070, Sirna_060
Whole Genome Sequencing
280 Accessions

Cicer bijugum (4)

Cicer echinospermum (63)
  6 at 30X Deep
  57 at 10X Shallow

Cicer reticulatum (161)
  20 at 30X Deep
  141 at 10X Shallow

Cicer arietinum (52)
  8 at 30X Deep
  44 at 10X Shallow
Whole Genome Sequencing
280 Accessions

Cicer echinospermum (63)  Cicer reticulatum (161)  Cicer arietinum (52)

8 at 30X Deep
CDCFrontier Dikbas Gocke Habru Minjar ICCV2 ICCV96029 ICC16207

44 at 10X Shallow
→ 17 Landraces & 35 Breeding Cultivars
Harvesting natural variation for climate resilience from crop wild progenitors

http://chickpealab.ucdavis.edu
Harvesting natural variation for climate resilience from crop wild progenitors

http://chickpealab.ucdavis.edu

Cultivated Material have very low Genetic Diversity
Harvesting natural variation for climate resilience from crop wild progenitors

http://chickpealab.ucdavis.edu

Wild Cicer really does have ~100X diversity

Cultivated Material have very low Genetic Diversity

theta_F (log10)
Harvesting natural variation for climate resilience from crop wild progenitors

Wild Cicer really does have ~100X diversity

Cicer echinospermum is nearly as diverse as Cicer reticulatum

Wild Relatives → Domestication → Regional diversification → Cultivated Material have very low Genetic Diversity

Cultivars

Landraces

http://chickpealab.ucdavis.edu
WGS allow deeper analyses of genomes

• GBS Representative Sequencing useful for understanding population structure and diversity
• WGS can characterize regions under selection
• Can use diploid information to estimate coalescence and population sizes
  – Independently from single diploid individuals
Population size and divergence of Cicer species using MCMC models

Years Before Present

Population Size in thousands (Ne)

Past
Present

Cicer echinospermum

Years Before Present

Population Size in thousands (Ne)
Population size and divergence of Cicer species using MCMC models.
Population size and divergence of Cicer species using MCMC models

Population size in thousands (Ne)

- **Cicer echinospermum**
- **Cicer reticulatum**

~120KYA
Population size and divergence of Cicer species using MCMC models

Cicer echinospermum
Cicer reticulatum

~120KYA

Years Before Present

Present
Population size and divergence of Cicer species using MCMC models

Population size in thousands (Ne)

Years Before Present

Present

Years Before Present

Past

Cicer echinospermum
Cicer reticulatum
Cicer arietinum (Elite Cultivars)

~120KYA
Population size and divergence of Cicer species using MCMC models
Population size and divergence of Cicer species using MCMC models

Population Size in thousands (Ne)

Years Before Present

Present

Years Before Present

Past

Cicer echinospermum
Cicer reticulatum
Cicer arietinum (Elite Cultivars)

~12KYA

~120KYA
Population size and divergence of Cicer species using MCMC models
f3 test shows introgression of Wild Cicer

26 wild accessions
52 cultivated accessions
→ ~34,000 combinations

Regardless of combination of wild, cultivated1, and cultivated2 being test, phylogeny holds!!!
f3 test shows introgression of Wild Cicer into Australian cultivars
f3 test shows introgression of Wild Cicer into Australian cultivars

Current work is underway to characterize these regions of the genome
SNP analyses reveal distinct chlorotypes

152 Chloroplast SNPs

61 Cicer echinospermum accessions
SUMMARY & FUTURE WORK

Non nuclear perspective into the genome of the Peter civilization, genomes Sirnak ancestry...
SUMMARY & FUTURE WORK

280

Non nuclear perspective into the genome of the

SUMMARY & FUTURE WORK
SUMMARY & FUTURE WORK

Non nuclear perspective into the genome of the...
Main Topics

• When was chickpea domesticated?
• How many times has domestication occur?
• What parts of the genomes have been selected?
• What are the mechanism for which selection has occurred?
Fay and Wu H identifies derived mutations

Negative numbers indicate excess of derived alleles
excess of derived mutations

Fay & Wu H

Purifying Selection

Derived mutations near fixation in population

Rare alleles

Tajima D

Intermediate alleles
excess of derived mutations

Intermediate alleles

Fay & Wu H

Derived mutations near fixation in population

Rare alleles

Tajima D

Intermediate alleles
Distribution of Fay & Wu H
Distribution of Fay & Wu H
Distribution of Fay & Wu H

Chromosome 1

Chromosome 2

Chromosome 4
How are these regions under selection?

49 regions, 25 MB, 2400 genes

Distribution of Fay & Wu H

Chromosome 1

Chromosome 4
Main Topics

• When was chickpea domesticated?
• How many times has domestication occur?
• What parts of the genomes have been selected?
• What are the mechanism for which selection has occurred?
Genomic Selection Sweeps

Beneficial mutation occurs OR
New environment selects for existing mutation
Genomic Selection Sweeps

Beneficial mutation occurs OR
New environment selects for existing mutation

Individuals with red allele are selected and are “swept” into the population
Genomic Selection Sweeps

Beneficial mutation occurs OR New environment selects for existing mutation

Individuals with red allele are selected and are “swept” into the population

Red allele is fixed in population and diversity is reduced
Genomic Selection Sweeps

## 13 Overlapping SNP Windows along Ca4: 15279875 - 15569136

<table>
<thead>
<tr>
<th>SNP Window</th>
<th>Genes</th>
</tr>
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<tbody>
<tr>
<td>15092467 - 15399468</td>
<td>CDCVanguard, ICCC32, ICCV88516, ICCV93512, ICCV93954, ICCV96029, ICCV96836</td>
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13 Overlapping SNP Windows along Ca4: 15279875 - 15569136
### 13 Overlapping SNP Windows along Ca4: 15279875 - 15569136

<table>
<thead>
<tr>
<th>SNP Windows</th>
<th>Overlapping SNP Windows</th>
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</thead>
<tbody>
<tr>
<td>15279875−15569136</td>
<td>101 SNPs in Window 3: 15379875−15421690</td>
</tr>
</tbody>
</table>

**Genome Position of Window**

**Frequency of Haplotype**

**Names**

- Amit
- CDC512–51
- CDCCorinne
- CDCLeader
- CDCLuna
- CDCVanguard
- Chefe
- Genesis090
- Gocke
- Habru
- HatTrick
- ICC32
- ICC83105
- ICCV2
- ICCV88202
- ICCV88516
- ICCV92311
- ICCV92337
- ICCV92944
- ICCV93512
- ICCV93952
- ICCV93954
- ICCV96029
- ICCV96836
- ICCV97105
- ICCV97105
- ILC3279
- JG62
- Myles
- Slasher
- YeZ1N

**Identifiers**

- BL
- Dikbas
- Minjar
- Pistol
13 Overlapping SNP Windows along Ca4: 15279875 - 15569136
13 Overlapping SNP Windows along Ca4: 15279875 - 15569136
Windows along Ca1: 637K – 1.45M
Windows along Ca1: 637K – 1.45M

<table>
<thead>
<tr>
<th>Frequency of Haplotype</th>
<th>Windows along Ca1: 637K – 1.45M</th>
</tr>
</thead>
<tbody>
<tr>
<td>101 SNPs in Window 8: 764680–785110</td>
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- Amit
- BL
- CDC512–51
- CDCCorinne
- CDCLeader
- CDCLuna
- CDCVanguard
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- Genesis090
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- HatTrick
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- ICCL83105
- ICCV2
- ICCV88202
- ICCV88516
- ICCV92311
- ICCV92337
- ICCV92944
- ICCV93512
- ICCV93944
- ICCV93952
- ICCV93954
- ICCV96029
- ICCV96836
- ICCV97105
- ILC3279
- JG62
- Minjar
- Myles
- YeZ1N

Pistol
Slasher
Windows along Ca1: 637K – 1.45M
Windows along Ca1: 35.0M – 35.5M
Distribution of Sweeps in Cultivars

Ca1 Position (MB)

Ca2 Position (MB)

Ca3 Position (MB)

Ca4 Position (MB)

Ca5 Position (MB)

Ca6 Position (MB)

Ca7 Position (MB)

Ca8 Position (MB)
Selection sweeps on chr1 in Cultivars
Selection sweeps on chr2 in Cultivars
Selection sweeps on chr3 in Cultivars
Selection sweeps on chr2 in Cultivars
Distribution of Sweeps in Cultivars

86 regions under selection sweeps
74/86 overlap with regions identified using D and H tests
37 Hard Sweeps, 62 Soft Sweeps
Distribution of Sweeps in Wilds
Sweep at Ca4: 1 – 300001
201 SNPs in Window 1: 14864 – 167913

Genome Position of Window
Frequency of Haplotype
Sweep at Ca4: 1 – 300001
201 SNPs in Window 8: 229246 – 388706
Sweep at Ca4: 1 – 300001
201 SNPs in Window 5: 167913 – 251993
Distribution of Sweeps in Wilds
Ca2: 27574443 – 29399524

Genome Position of Window
Sweep at Ca2: 27574443 – 29399524
201 SNPs in Window 57: 28538133 – 28575174

<table>
<thead>
<tr>
<th>Genome Position of Window</th>
<th>Frequency of Haplotype</th>
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<tbody>
<tr>
<td>27574443 − 29399524</td>
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</table>

*Names of individuals and SNPs in the window.*
Main Topics

• When was chickpea domesticated?
  – Beginning at 10KYA

• How many times has domestication occur?
  – Cultivars have been domesticated at least 3X

• What parts of the genomes have been selected?
  – 49 regions, 25 MB, 2400 genes

• What are the mechanism for which selection
  has occurred?
  – 86 regions under selection sweeps