Subindividual Variation

Raymond L. Tremblay
University of Puerto Rico
Dept of Biology

Objective

- **Variation is everywhere!!**
    - Individuals vary in their mean
    - Individuals vary in time
    - Individuals vary in space
    - **Sub Individuals variation**

My goal for the week is demonstrate that

a) subindividual variation in individuals is the norm,

b) that we can measure such variation

c) determine if variation are significantly different among individuals and

d) subsequently show that phenotypic selection is another variable which can be included in the phenotypic selection studies.

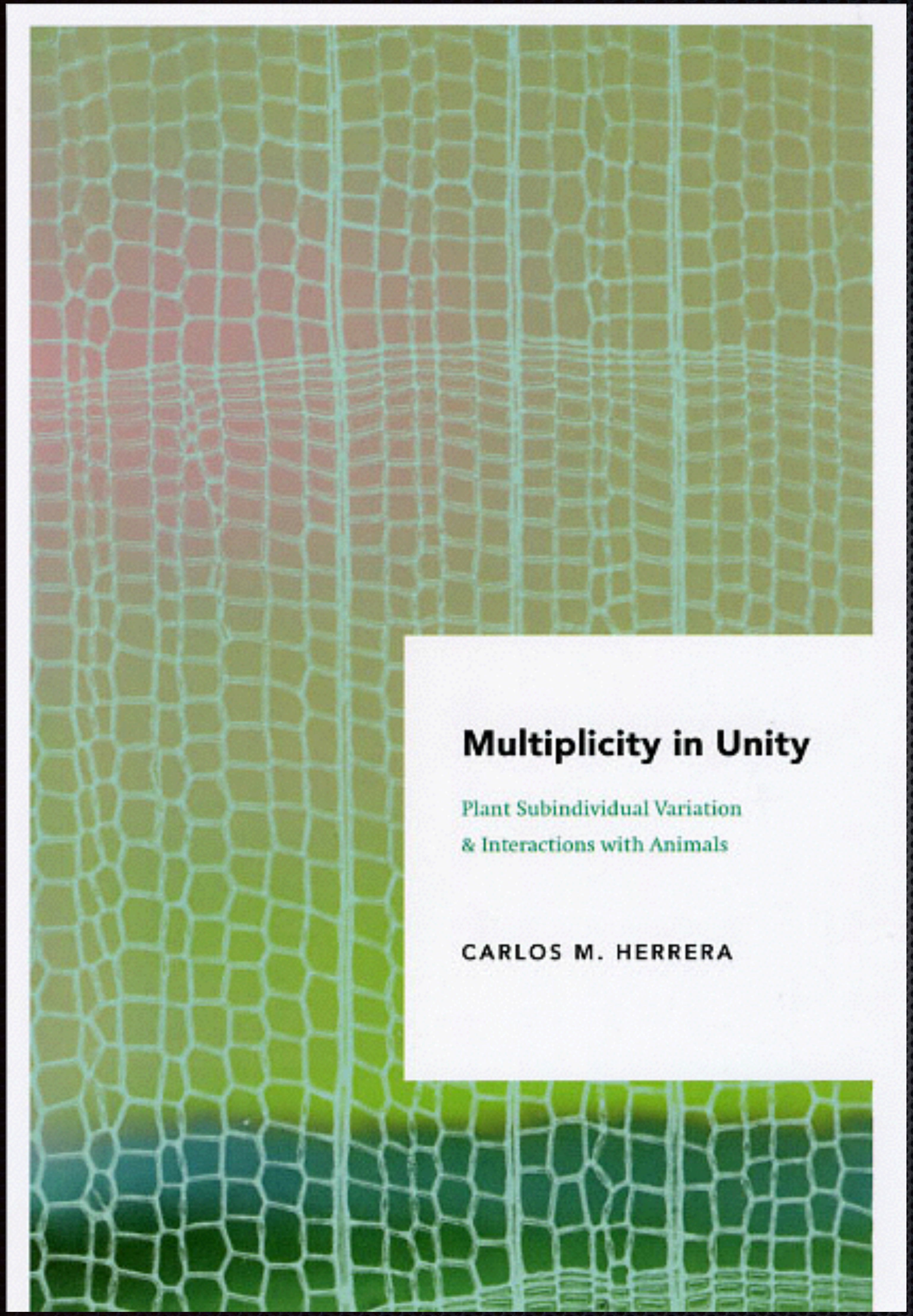
google “subindividual variation”

What is required for Natural Selection?

- 1. Variation in phenotypic characteristics
- 2. Genetic basis for the variation
- 3. Differential fitness among the variants

Alfred Russel Wallace

Measuring Phenotypic selection at different scales



Multiplicity in Unity

Plant Subindividual Variation
& Interactions with Animals

CARLOS M. HERRERA

- **Phenotypic selection**
  - Selection for the mean
  - **Selection for variation**
  - Selection for other indices of variation
    - **Skewness**
    - **Kurtosis**

Reiterated structures and variation

- Plants are variable organisms
    - Theophrastus 371-287 BC
        - The leaves "of the abele ivy and of the plant called kroton are unlike one another and of different forms"

Enquiry into Plants, book 1

Early works on variation

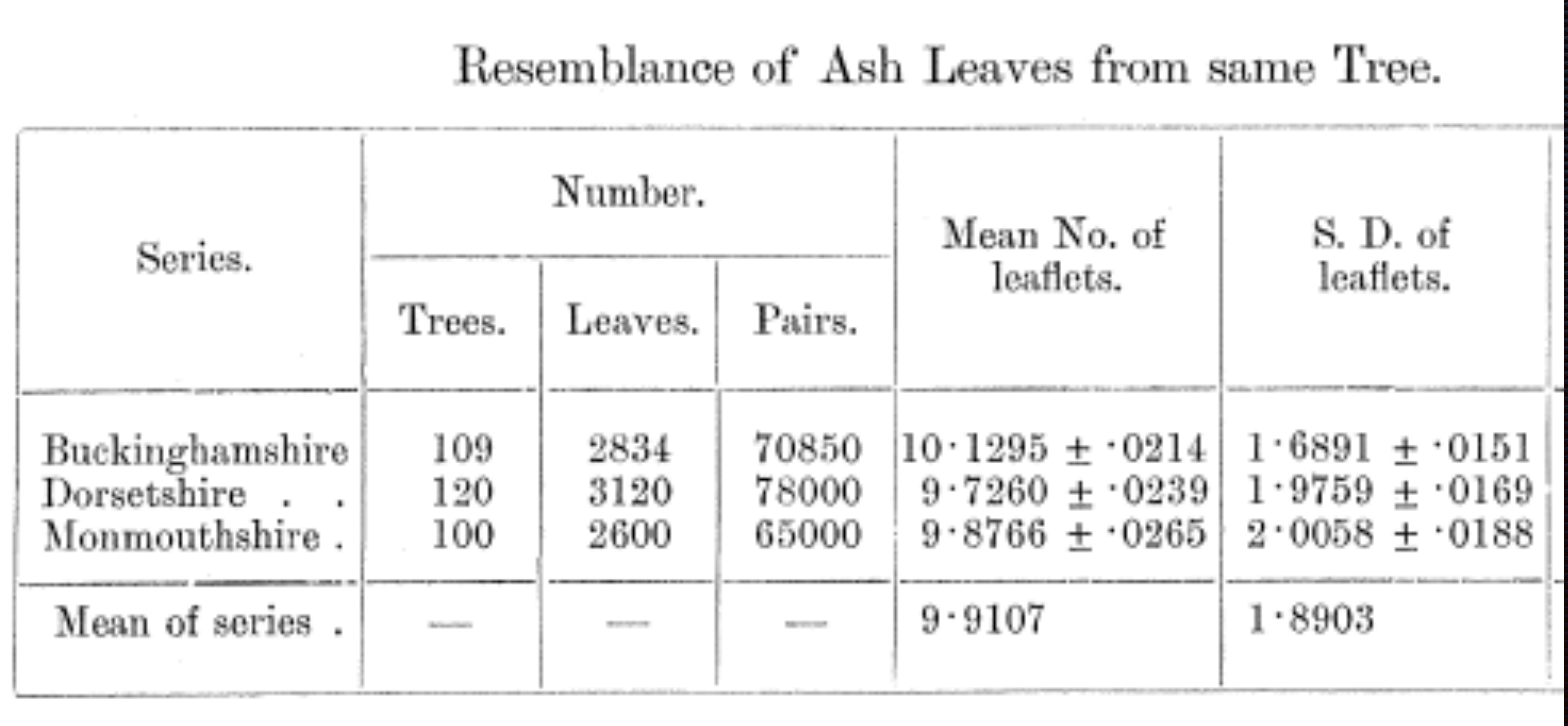
- Karl Pearson 1901:
- *On the Principle of Homotyposis and Its Relation to Heredity, to the Variability of the Individual, and to that of the Race. Part I. Homotypos in the Vegetable Kingdom.*
- *vol. 197: 287-399*
- *Philosophical Transactions of the Royal Society A*

- a. What is the ratio of individual to racial variability?
- b. How is the variability in the individual related to inheritance within the race?

Fraxinus excelsior, Ash

26 leaves per tree at 3 different sites

Variation among Sites

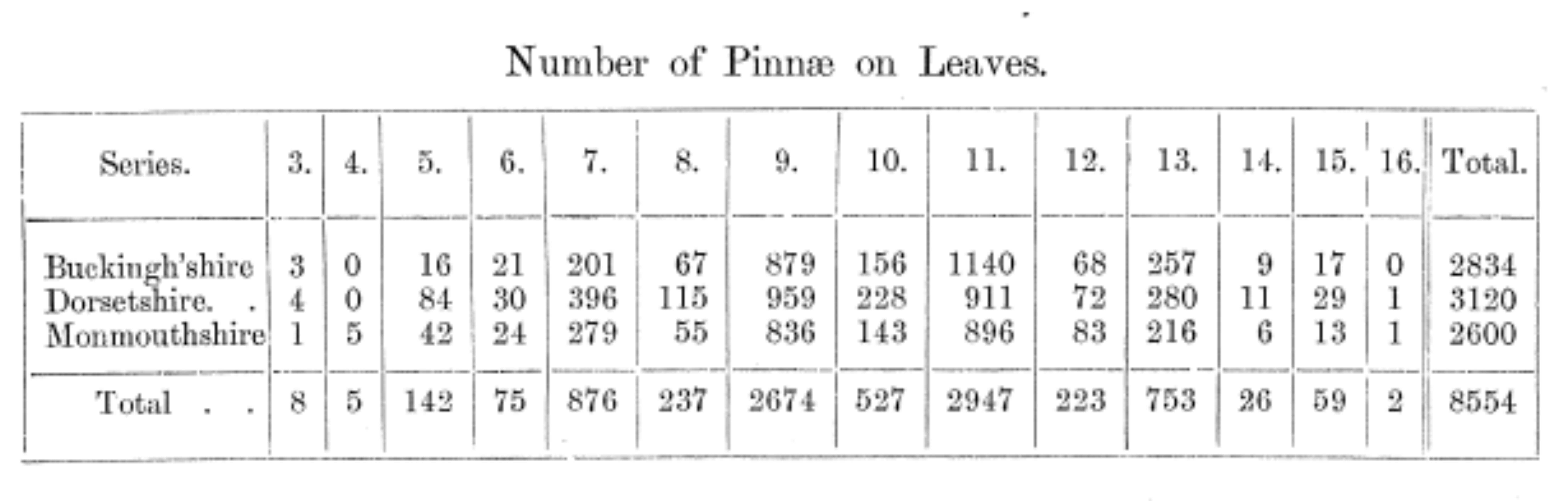


Resemblance of Ash Leaves from same Tree.

Series.	Number.			Mean No. of leaflets.	S. D. of leaflets.
	Trees.	Leaves.	Pairs.		
Buckinghamshire	109	2834	70850	10·1295 ± ·0214	1·6891 ± ·0151
Dorsetshire . .	120	3120	78000	9·7260 ± ·0239	1·9759 ± ·0169
Monmouthshire .	100	2600	65000	9·8766 ± ·0265	2·0058 ± ·0188
Mean of series .	—	—	—	9·9107	1·8903

Pearson 1901

Frequency Distribution number of leaf pinnae by site



Number of Pinnæ on Leaves.

Series.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	Total.
Buckingh'shire	3	0	16	21	201	67	879	156	1140	68	257	9	17	0	2834
Dorsetshire. .	4	0	84	30	396	115	959	228	911	72	280	11	29	1	3120
Monmouthshire	1	5	42	24	279	55	836	143	896	83	216	6	13	1	2600
Total . .	8	5	142	75	876	237	2674	527	2947	223	753	26	59	2	8554

	3	4	5	6	7	8	9	10	11	12	13	14	15	16
B	0.001	0.000	0.006	0.007	0.071	0.024	0.31	0.055	**0.402**	0.024	0.091	0.003	0.006	0.000
D	0.001	0.000	0.030	0.011	0.140	0.041	**0.338**	0.080	0.321	0.025	0.099	0.004	0.010	0.000
M	0.000	0.002	0.015	0.008	0.098	0.019	0.295	0.050	**0.316**	0.029	0.076	0.002	0.005	0.000

Frequency number of sepals in *Anemone nemorosa* (Yule 1902)

- Gathered data from 1000 individuals at three different sites in 1899-1900.

Biometrika 1: 307-309

Sepal **(Tepals)** Number in *Anemone nemorosa*

tepals = 6

tepals = 9

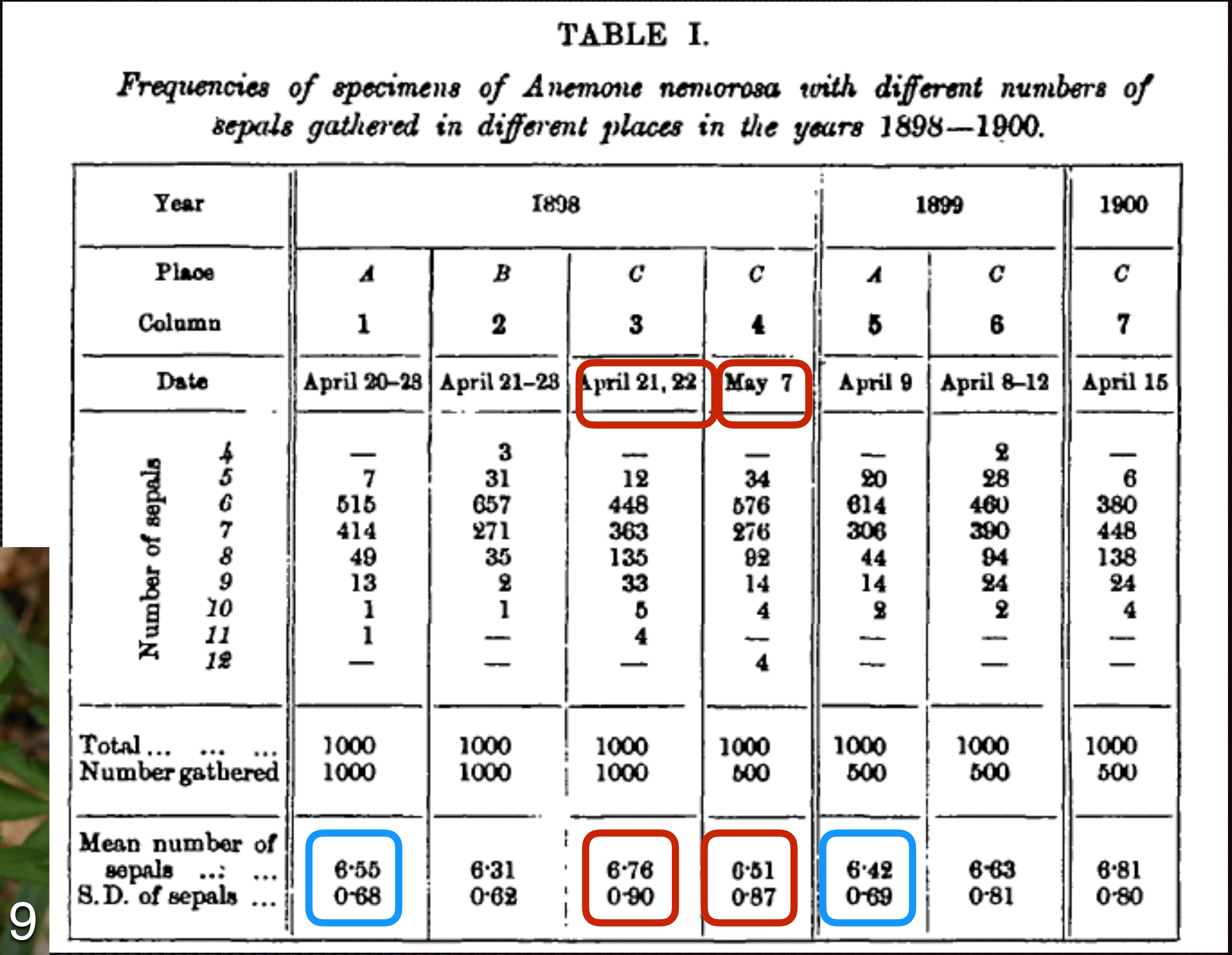


TABLE I.

Frequencies of specimens of Anemone nemorosa with different numbers of sepals gathered in different places in the years 1898—1900.

Year	1898				1899		1900
Place	*A*	*B*	*C*	*C*	*A*	*C*	*C*
Column	1	2	3	4	5	6	7
Date	April 20–28	April 21–28	April 21, 22	May 7	April 9	April 8–12	April 15
Number of sepals *4*	—	3	—	—	—	2	—
5	7	31	12	34	20	28	6
6	515	657	448	576	614	460	380
7	414	271	363	276	306	390	448
8	49	35	135	92	44	94	138
9	13	2	33	14	14	24	24
10	1	1	5	4	2	2	4
11	1	—	4	—	—	—	—
12	—	—	—	4	—	—	—
Total	1000	1000	1000	1000	1000	1000	1000
Number gathered	1000	1000	1000	500	500	500	500
Mean number of sepals	6·55	6·31	6·76	6·51	6·42	6·63	6·81
S.D. of sepals ...	0·68	0·62	0·90	0·87	0·69	0·81	0·80

Number of stamens

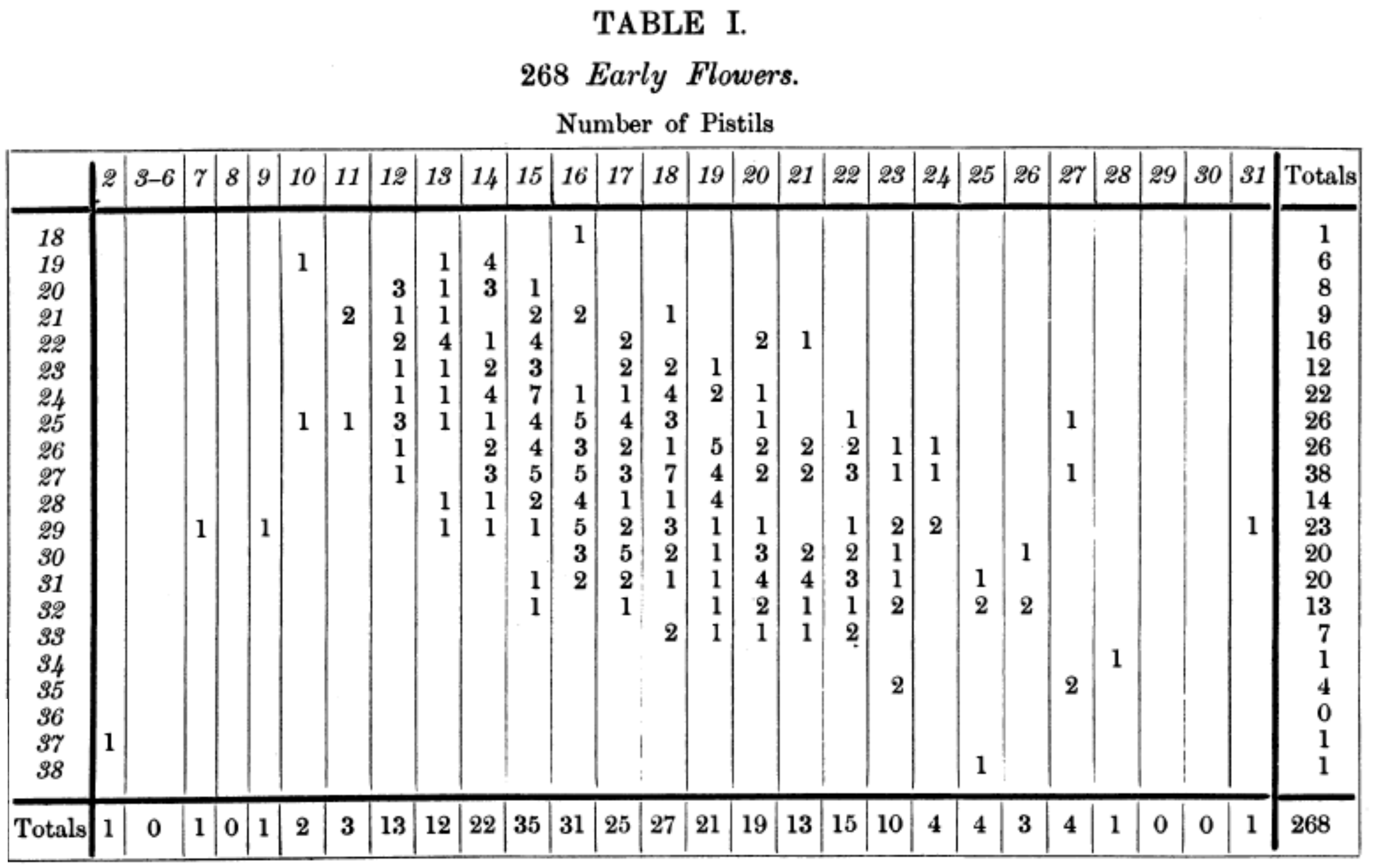


TABLE I.

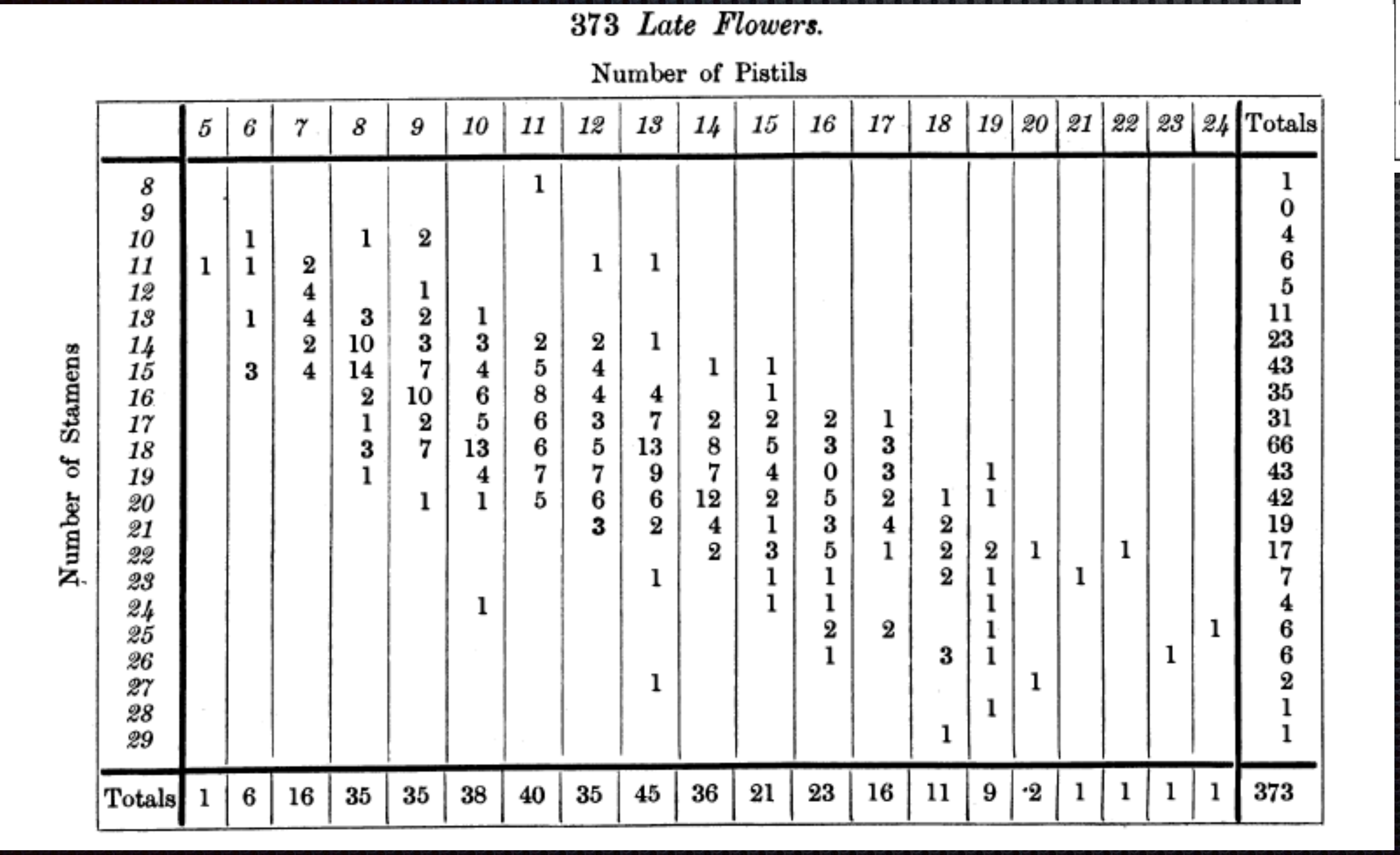
268 *Early Flowers.*

Number of Pistils

Number of Stamens

	2	3–6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals
18												1																1
19						1			1	4																		6
20								3	1	3	1																	8
21							2	1	1		2	2		1														9
22								2	4	1	4		2			2	1											16
23								1	1	2	3		2	2	1													12
24								1	1	4	7	1	1	4	2	1												22
25						1	1	3	1	1	4	5	4	3		1		1					1					26
26								1		2	4	3	2	1	5	2	2	2	1	1								26
27								1		3	5	5	3	7	4	2	2	3	1	1			1					38
28									1	1	2	4	1	1	4													14
29			1		1				1	1	1	5	2	3	1	1		1	2	2							1	23
30												3	5	2	1	3	2	2	1			1						20
31											1	2	2	1	1	4	4	3	1		1							20
32											1		1		1	2	1	1	2		2	2						13
33														2	1	1	1	2										7
34																								1				1
35																			2				2					4
36																												0
37	1																											1
38																					1							1
Totals	1	0	1	0	1	2	3	13	12	22	35	31	25	27	21	19	13	15	10	4	4	3	4	1	0	0	1	268

Number of pistils



373 *Late Flowers.*

Number of Pistils

Number of Stamens

	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	Totals
8							1														1
9																					0
10		1		1	2																4
11	1	1	2					1	1												6
12			4		1																5
13		1	4	3	2	1															11
14			2	10	3	3	2	2	1												23
15		3	4	14	7	4	5	4		1	1										43
16				2	10	6	8	4	4		1										35
17				1	2	5	6	3	7	2	2	2	1								31
18				3	7	13	6	5	13	8	5	3	3								66
19				1		4	7	7	9	7	4	0	3		1						43
20					1	1	5	6	6	12	2	5	2	1	1						42
21								3	2	4	1	3	4	2							19
22										2	3	5	1	2	2	1		1			17
23									1		1	1		2	1		1				7
24						1					1	1			1						4
25												2	2		1					1	6
26												1		3	1				1		6
27									1							1					2
28															1						1
29														1							1
Totals	1	6	16	35	35	38	40	35	45	36	21	23	16	11	9	·2	1	1	1	1	373

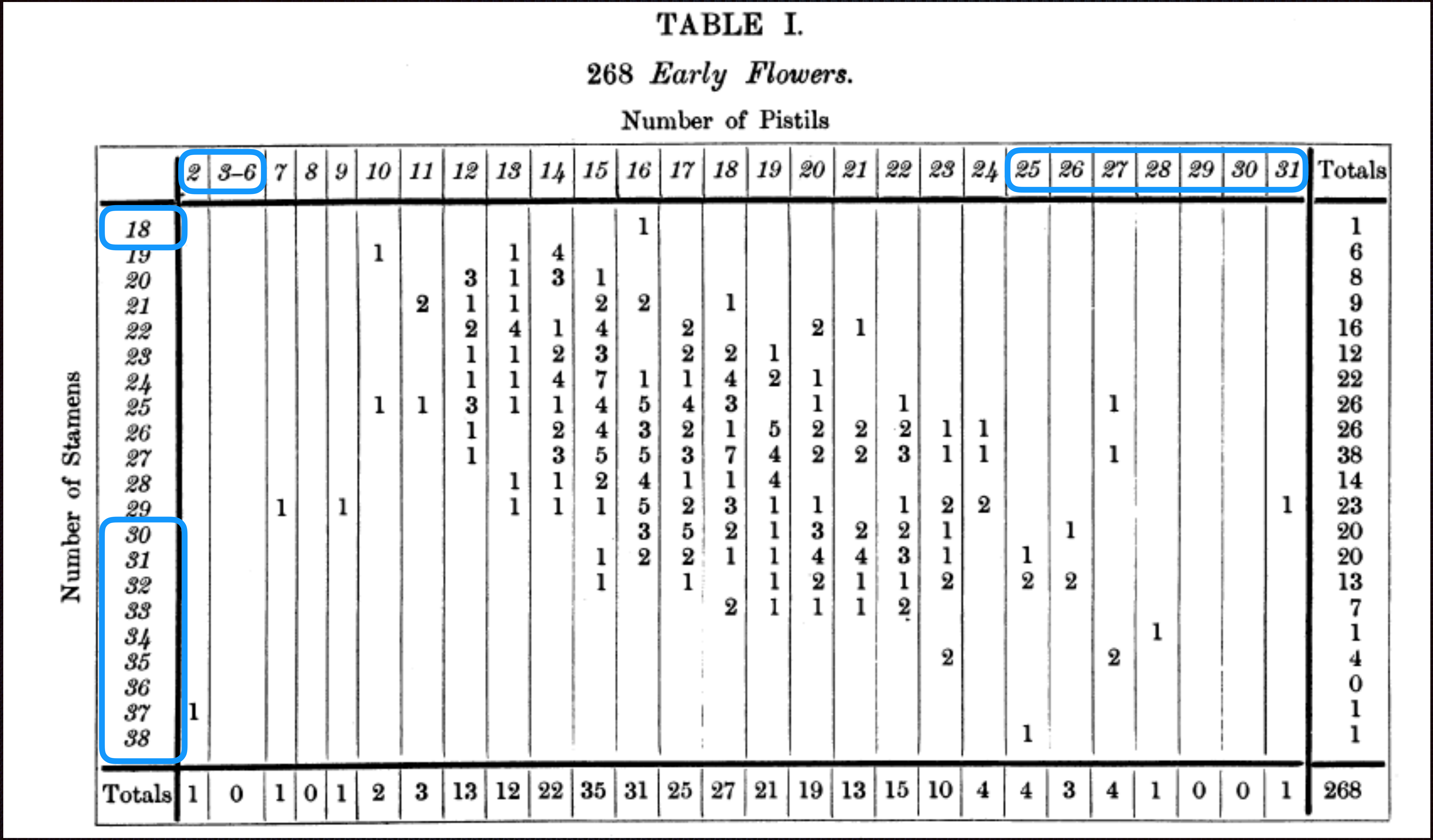


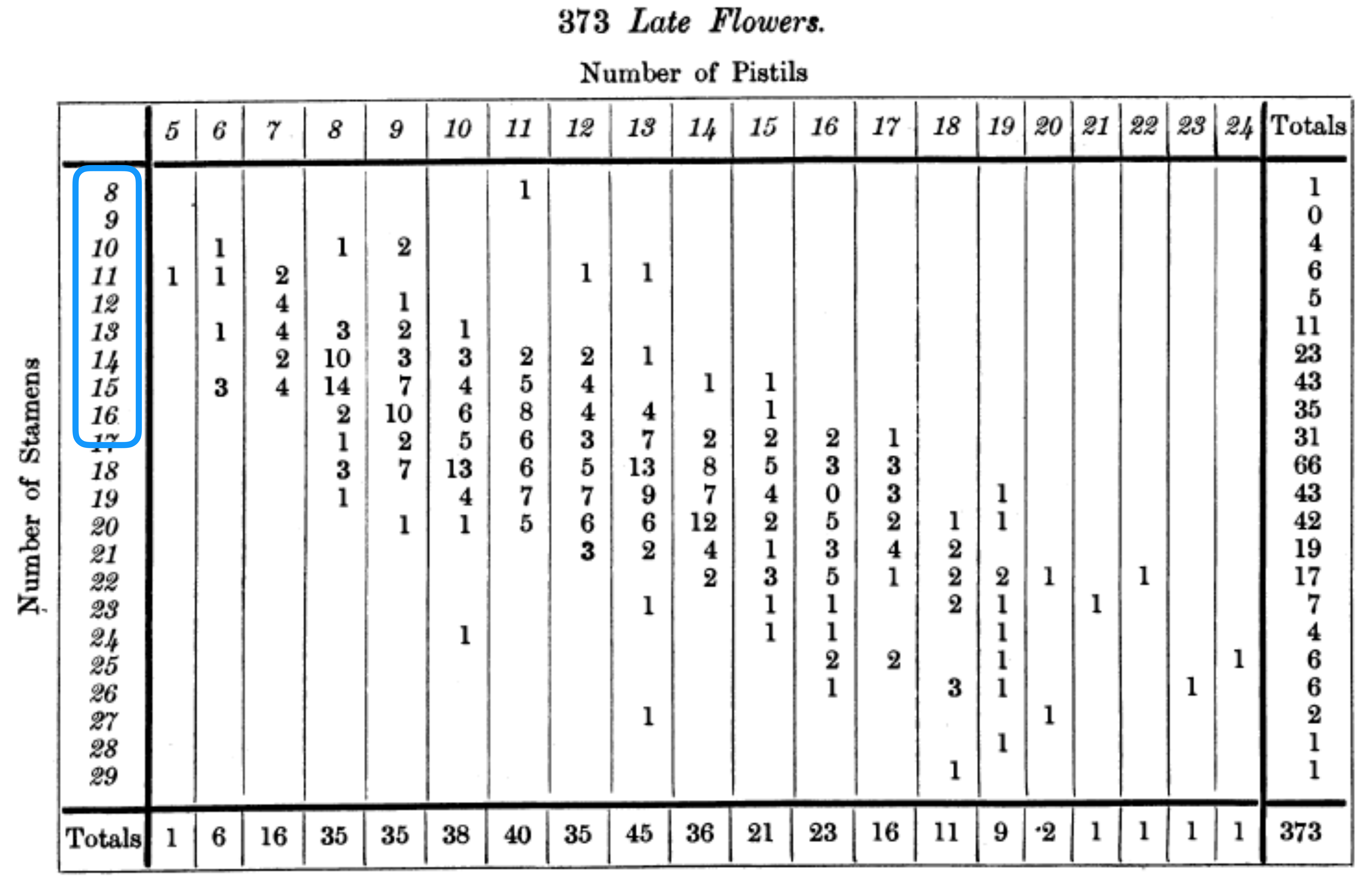
TABLE I.

268 *Early Flowers.*

Number of Pistils

Number of Stamens

	2	3–6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Totals
18												1																1
19						1			1	4																		6
20								3	1	3	1																	8
21							2	1	1		2	2		1														9
22								2	4	1	4		2			2	1											16
23								1	1	2	3		2	2	1													12
24								1	1	4	7	1	1	4	2	1												22
25						1	1	3	1	1	4	5	4	3		1		1					1					26
26								1		2	4	3	2	1	5	2	2	2	1	1								26
27								1		3	5	5	3	7	4	2	2	3	1	1			1					38
28									1	1	2	4	1	1	4													14
29			1		1				1	1	1	5	2	3	1	1		1	2	2							1	23
30												3	5	2	1	3	2	2	1			1						20
31											1	2	2	1	1	4	4	3	1		1							20
32											1		1		1	2	1	1	2		2	2						13
33														2	1	1	1	2										7
34																								1				1
35																			2				2					4
36																												0
37	1																											1
38																					1							1
Totals	1	0	1	0	1	2	3	13	12	22	35	31	25	27	21	19	13	15	10	4	4	3	4	1	0	0	1	268



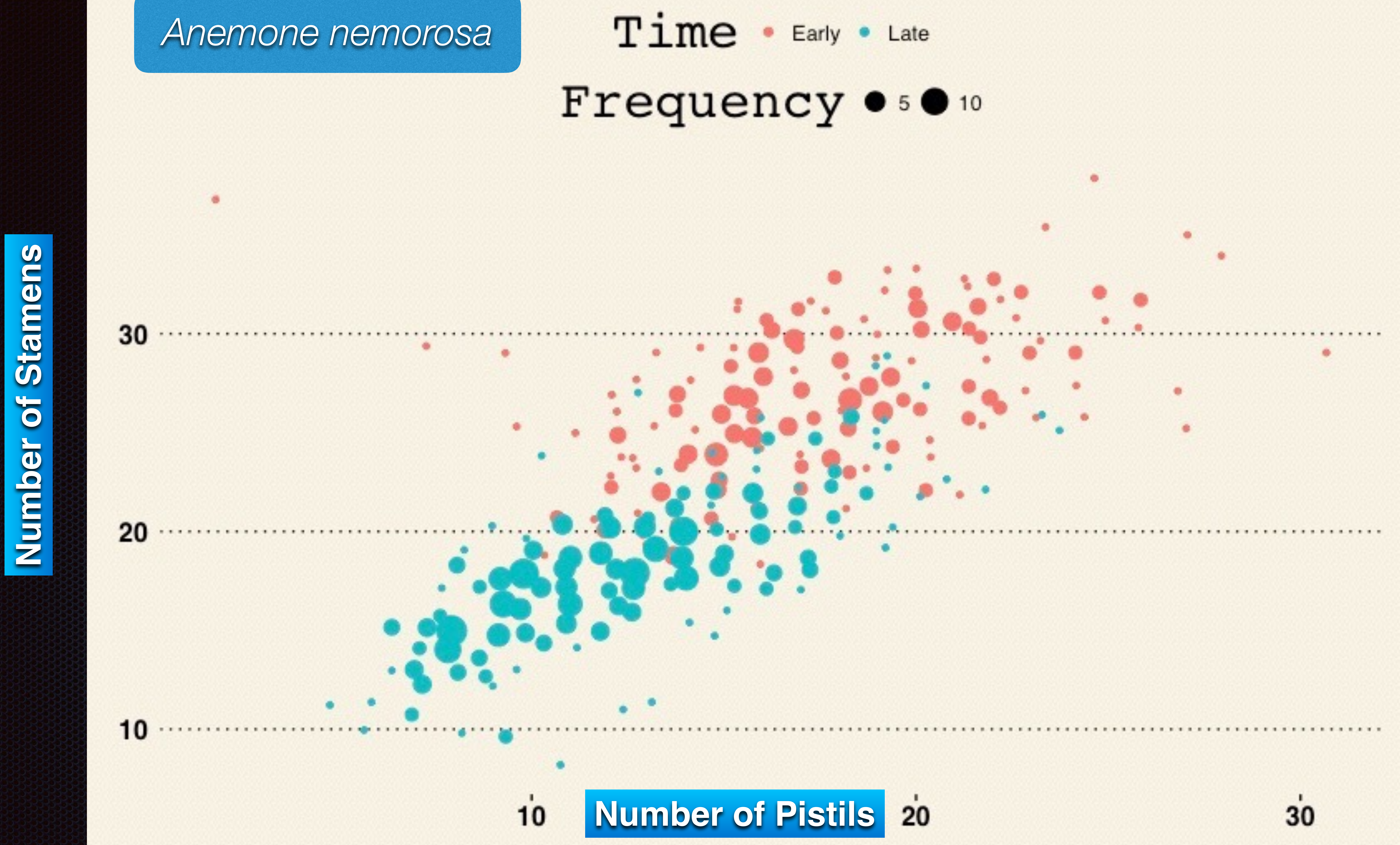
373 *Late Flowers.*

Number of Pistils

Number of Stamens

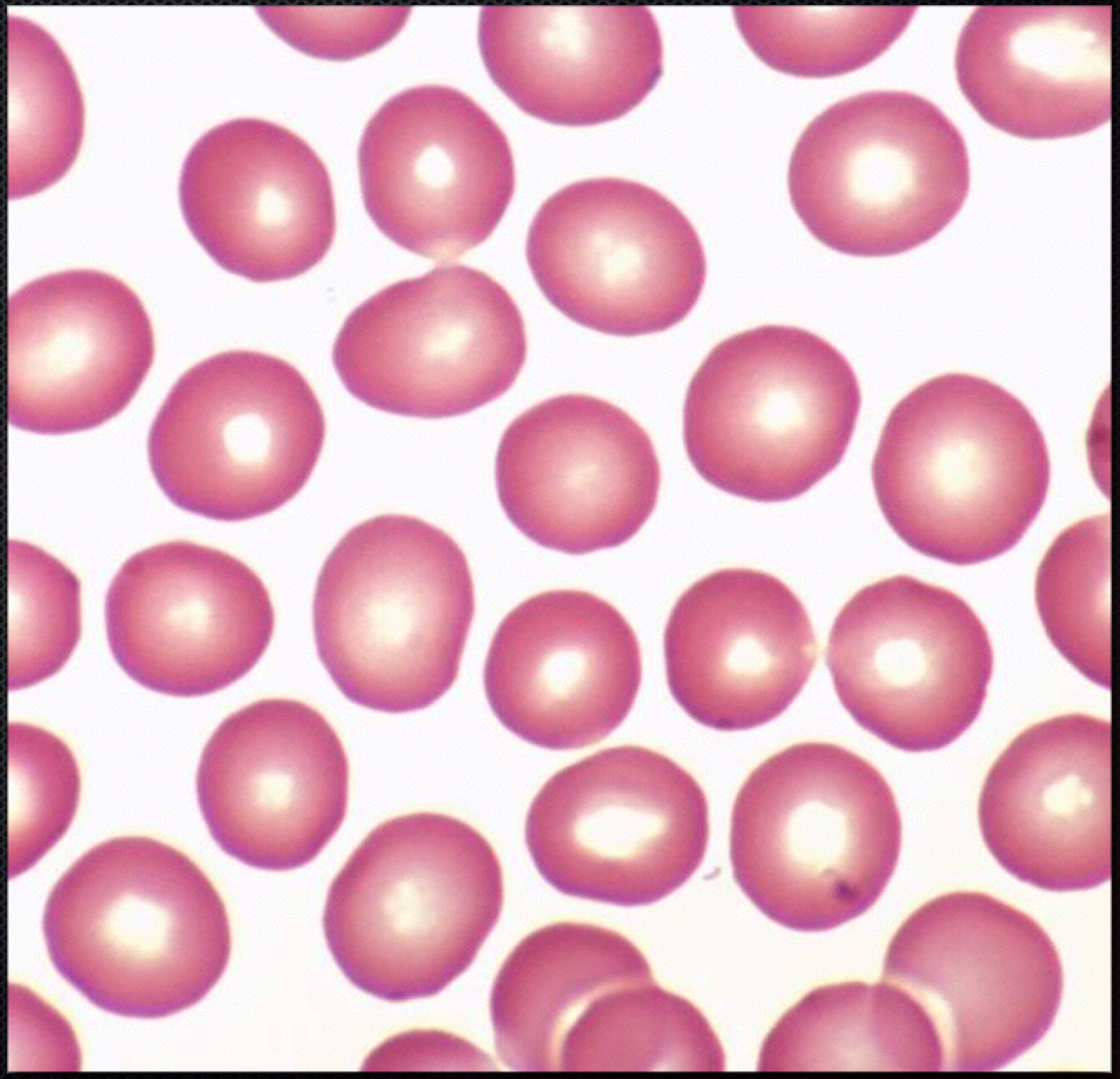
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	Totals
8							1														1
9																					0
10		1		1	2																4
11	1	1	2					1	1												6
12			4		1																5
13		1	4	3	2	1															11
14			2	10	3	3	2	2	1												23
15		3	4	14	7	4	5	4		1	1										43
16				2	10	6	8	4	4		1										35
17				1	2	5	6	3	7	2	2	2	1								31
18				3	7	13	6	5	13	8	5	3	3								66
19				1		4	7	7	9	7	4	0	3		1						43
20					1	1	5	6	6	12	2	5	2	1	1						42
21								3	2	4	1	3	4	2							19
22										2	3	5	1	2	2	1		1			17
23									1		1	1		2	1		1				7
24						1					1	1			1						4
25												2	2		1					1	6
26												1		3	1				1		6
27									1							1					2
28															1						1
29														1							1
Totals	1	6	16	35	35	38	40	35	45	36	21	23	16	11	9	2	1	1	1	1	373

Anemone nemorosa



Variation in red blood cell in 100 healthy individuals

- Measured 500 cells from 100 individuals



Price-Jones, C. "Red cell diameters in one hundred healthy persons and in pernicious anaemia: the effect of liver treatment." *The Journal of Pathology and Bacteriology* 32.3 (1929): 479-501.

Mean of the individuals

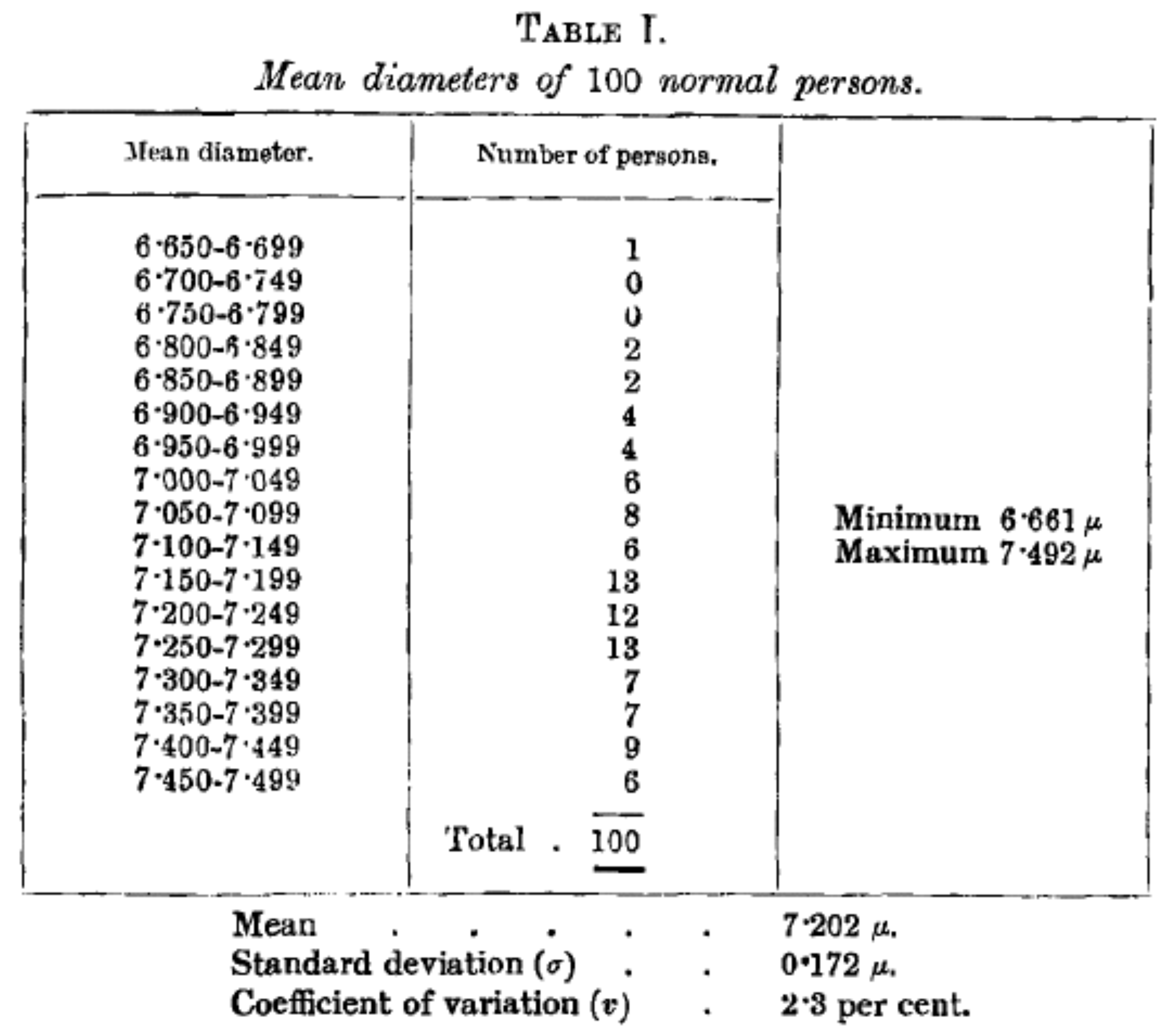


TABLE I.

Mean diameters of 100 normal persons.

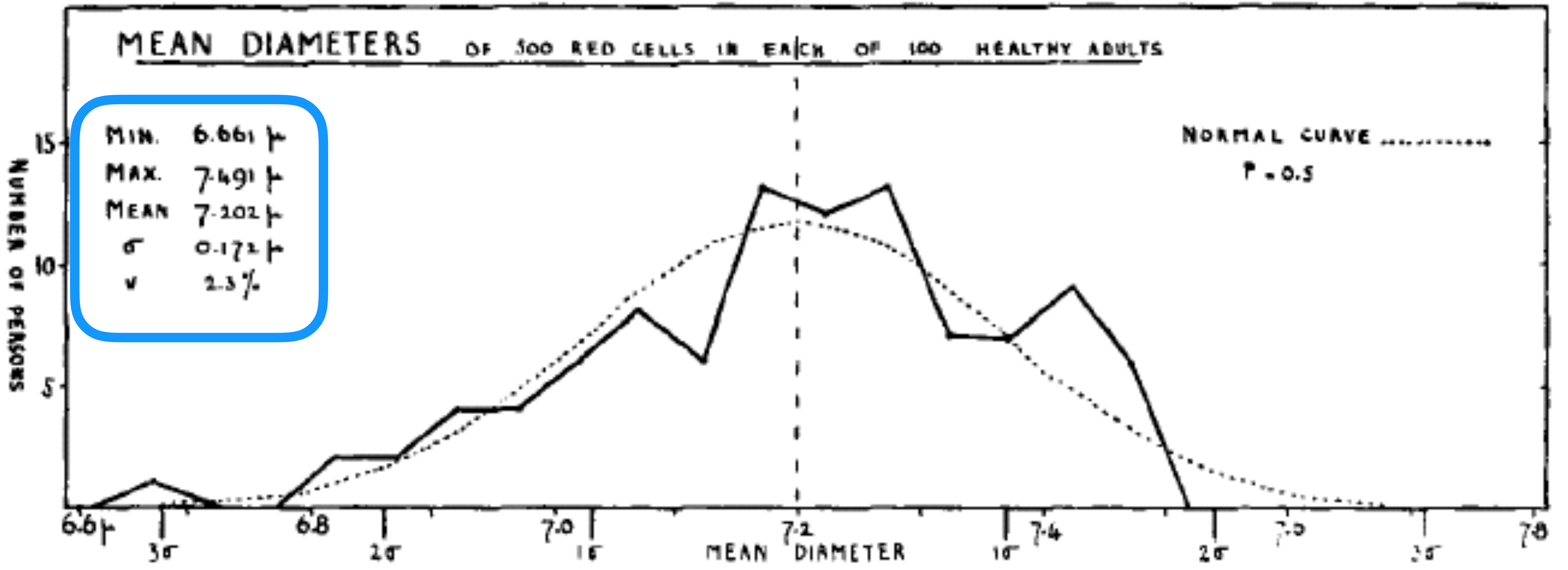
Mean diameter.	Number of persons.	
6·650-6·699	1	
6·700-6·749	0	
6·750-6·799	0	
6·800-6·849	2	
6·850-6·899	2	
6·900-6·949	4	
6·950-6·999	4	
7·000-7·049	6	
7·050-7·099	8	Minimum 6·661 μ
7·100-7·149	6	Maximum 7·492 μ
7·150-7·199	13	
7·200-7·249	12	
7·250-7·299	13	
7·300-7·349	7	
7·350-7·399	7	
7·400-7·449	9	
7·450-7·499	6	
	Total . 100	

Mean . . . . . 7·202 μ.
Standard deviation (σ) . . 0·172 μ.
Coefficient of variation (v) . 2·3 per cent.

Price-Jones, C. "Red cell diameters in one hundred healthy persons and in pernicious anaemia: the effect of liver treatment." *The Journal of Pathology and Bacteriology* 32.3 (1929): 479-501.

Mean Diameter of red blood cells

FIG. 1



Measure of variability, Coefficient of variation vs. variance

Pearson 1901: Phil Tran Royal
Society of London A 197: 285-379

$$CV = \frac{s}{\overline{x}} * 100$$

$$CV^* = (1 + \frac{1}{4n}) * CV$$

Unbiased estimate for small and medium sample size

A dimensionless number.

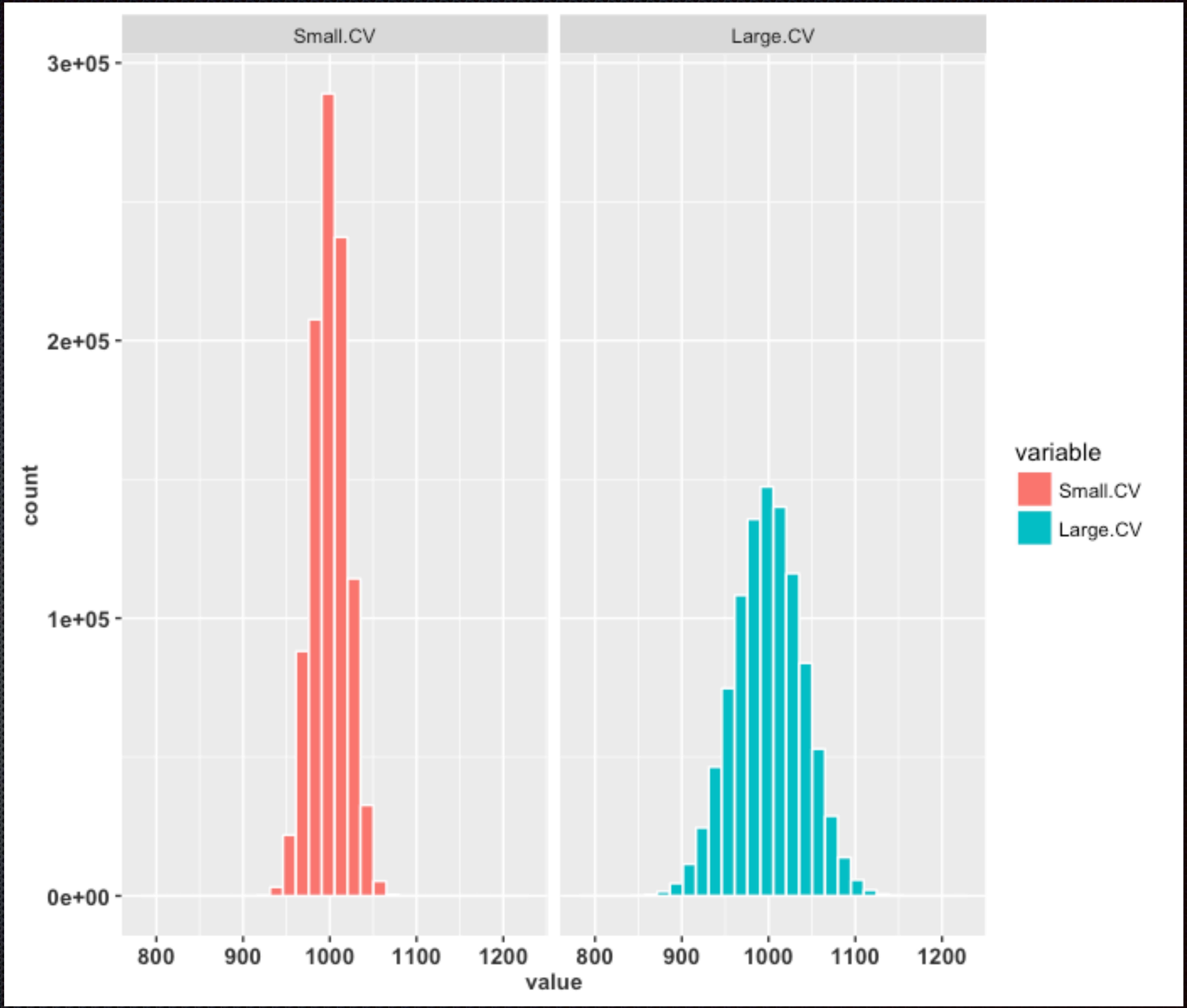
Advantage: For comparison between data sets with different units or *widely* different means, one should use the coefficient of variation instead of the standard deviation.

Disadvantage: When the mean value is close to zero, the coefficient of variation will approach infinity and is therefore sensitive to small changes in the mean

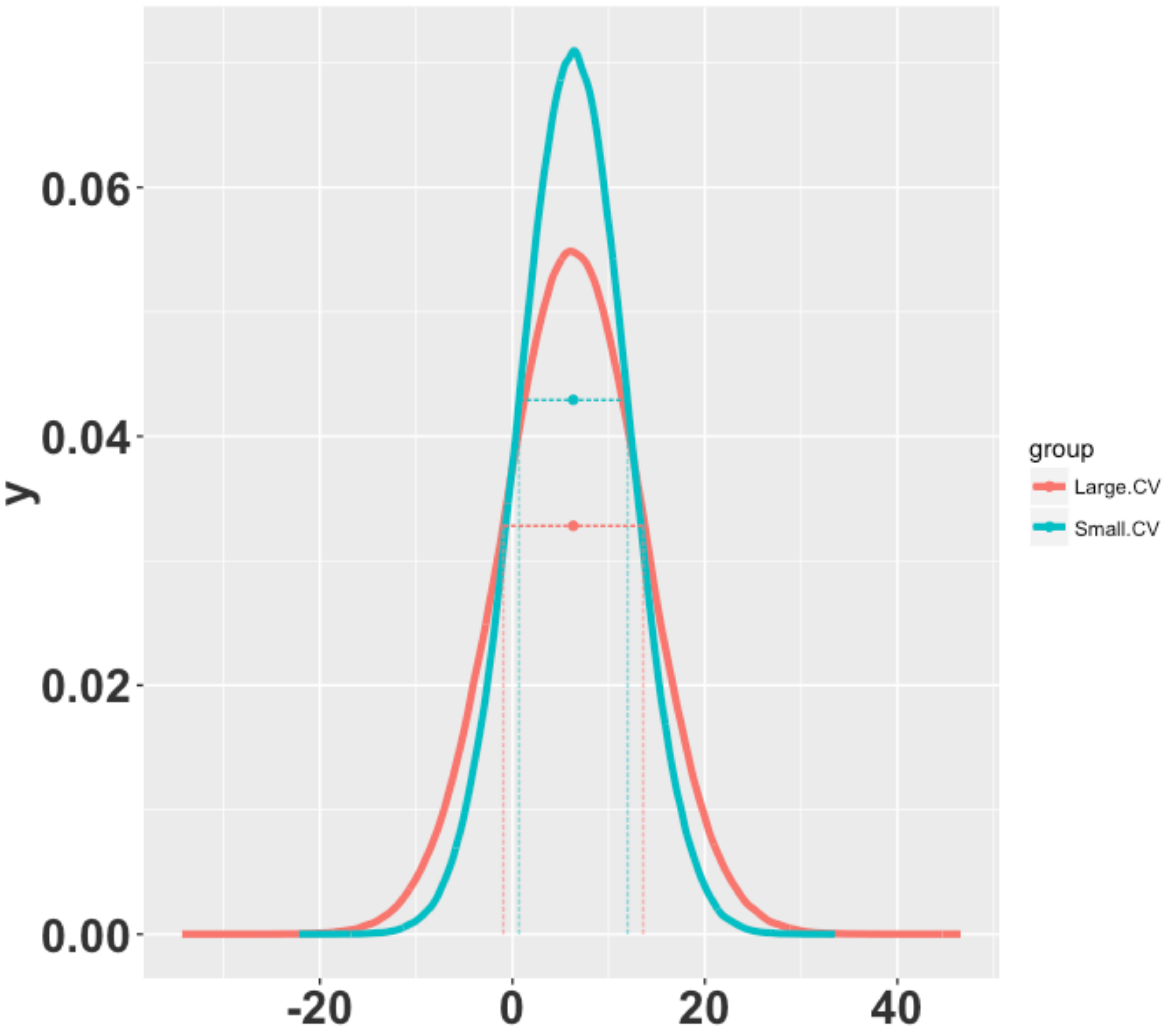
Pearson 1901: Phil Tran Royal Society of London A 197: 285-379

- “Measures of the absolute variation as given by the standard deviation seem to me of no use when we are comparing different characters in different species”

Coeffcient of Variation of two normally distributed data set



Individuals can differ in the amount of variation



Coefficient of variation

Coefficient of Variation

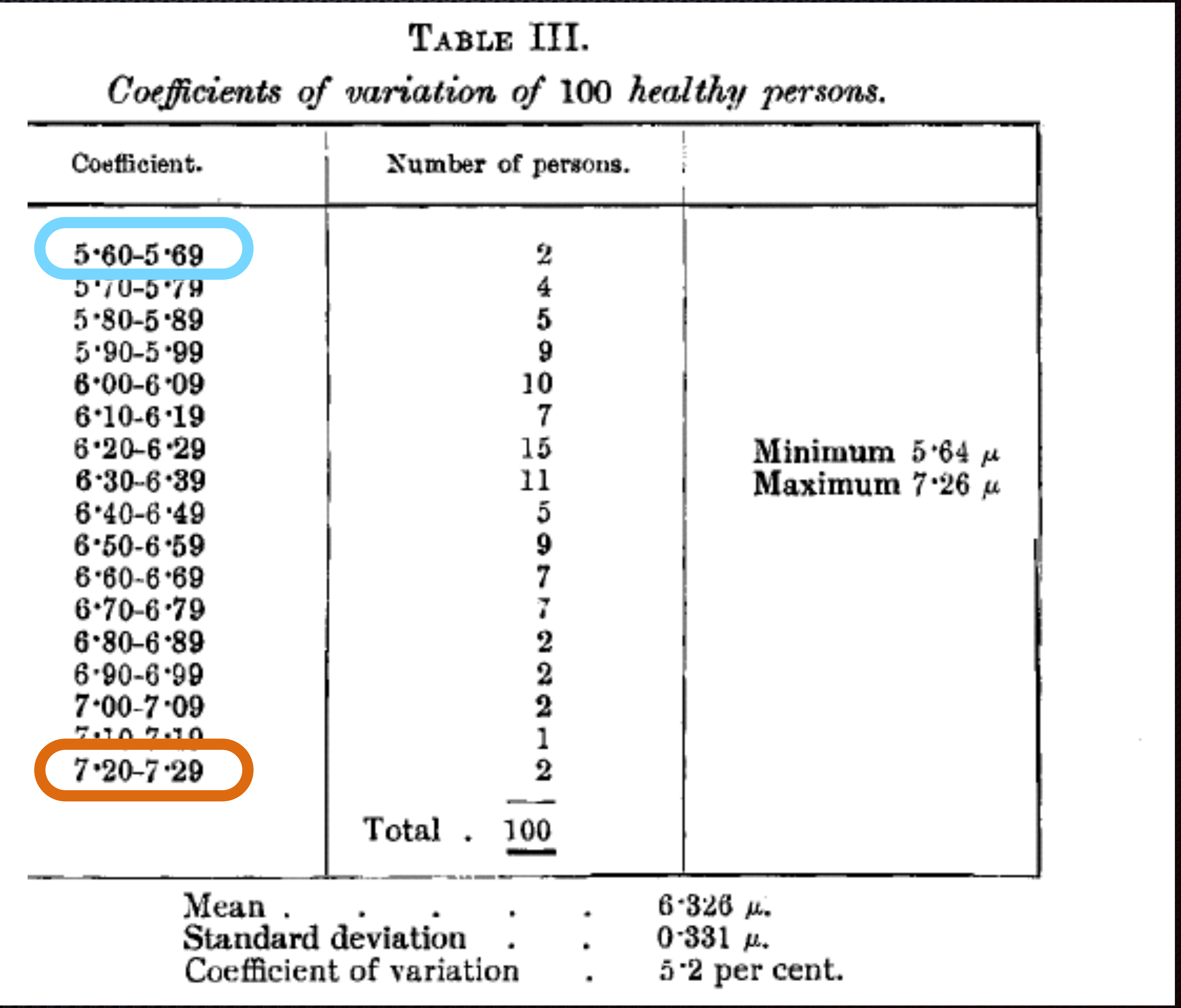


TABLE III.

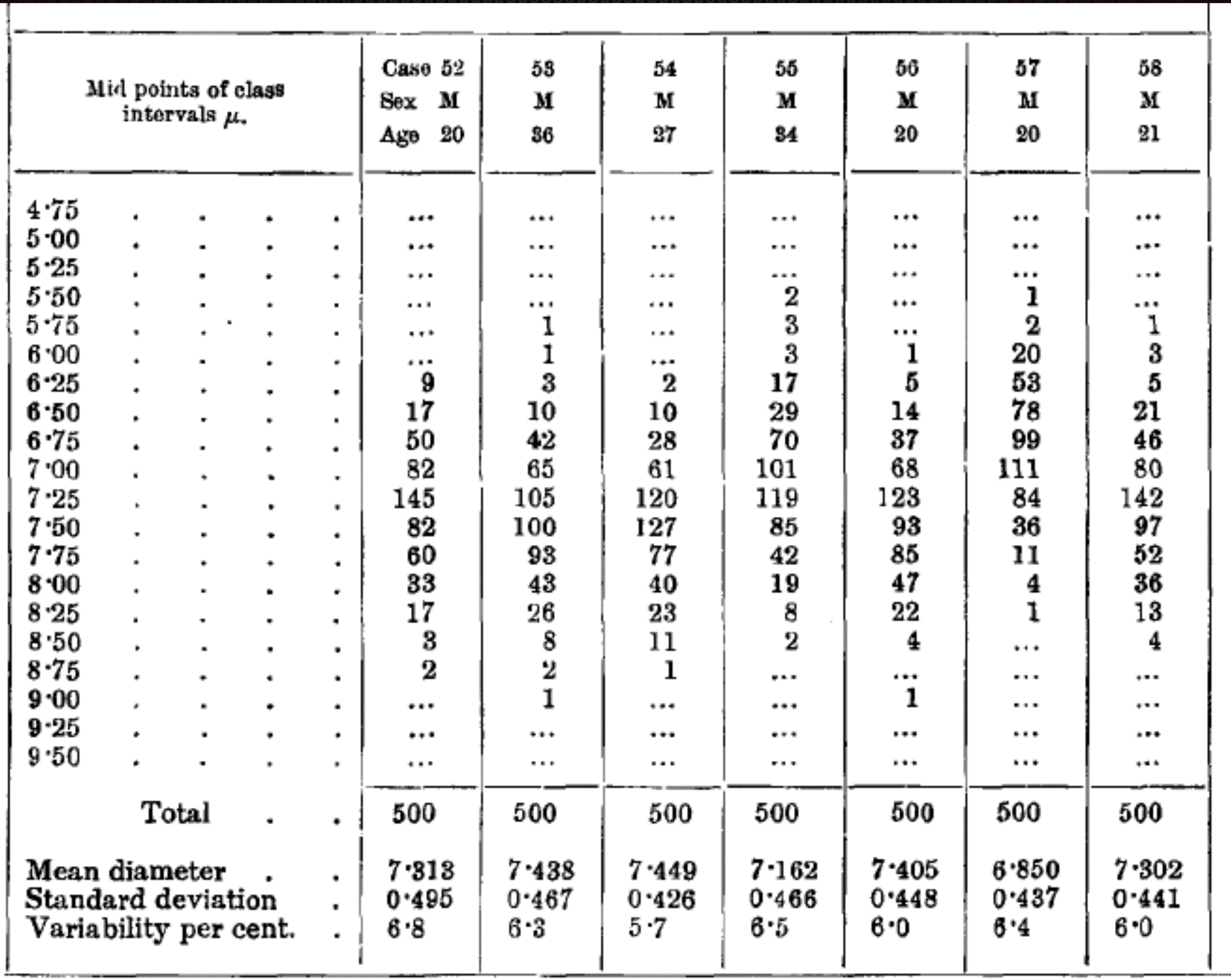
Coefficients of variation of 100 healthy persons.

Coefficient.	Number of persons.	
5·60-5·69	2	
5·70-5·79	4	
5·80-5·89	5	
5·90-5·99	9	
6·00-6·09	10	
6·10-6·19	7	
6·20-6·29	15	Minimum 5·64 μ
6·30-6·39	11	Maximum 7·26 μ
6·40-6·49	5	
6·50-6·59	9	
6·60-6·69	7	
6·70-6·79	7	
6·80-6·89	2	
6·90-6·99	2	
7·00-7·09	2	
7·10-7·19	1	
7·20-7·29	2	
Total .	100	

Mean . . . . . . 6·326 μ.
Standard deviation . . 0·331 μ.
Coefficient of variation . 5·2 per cent.

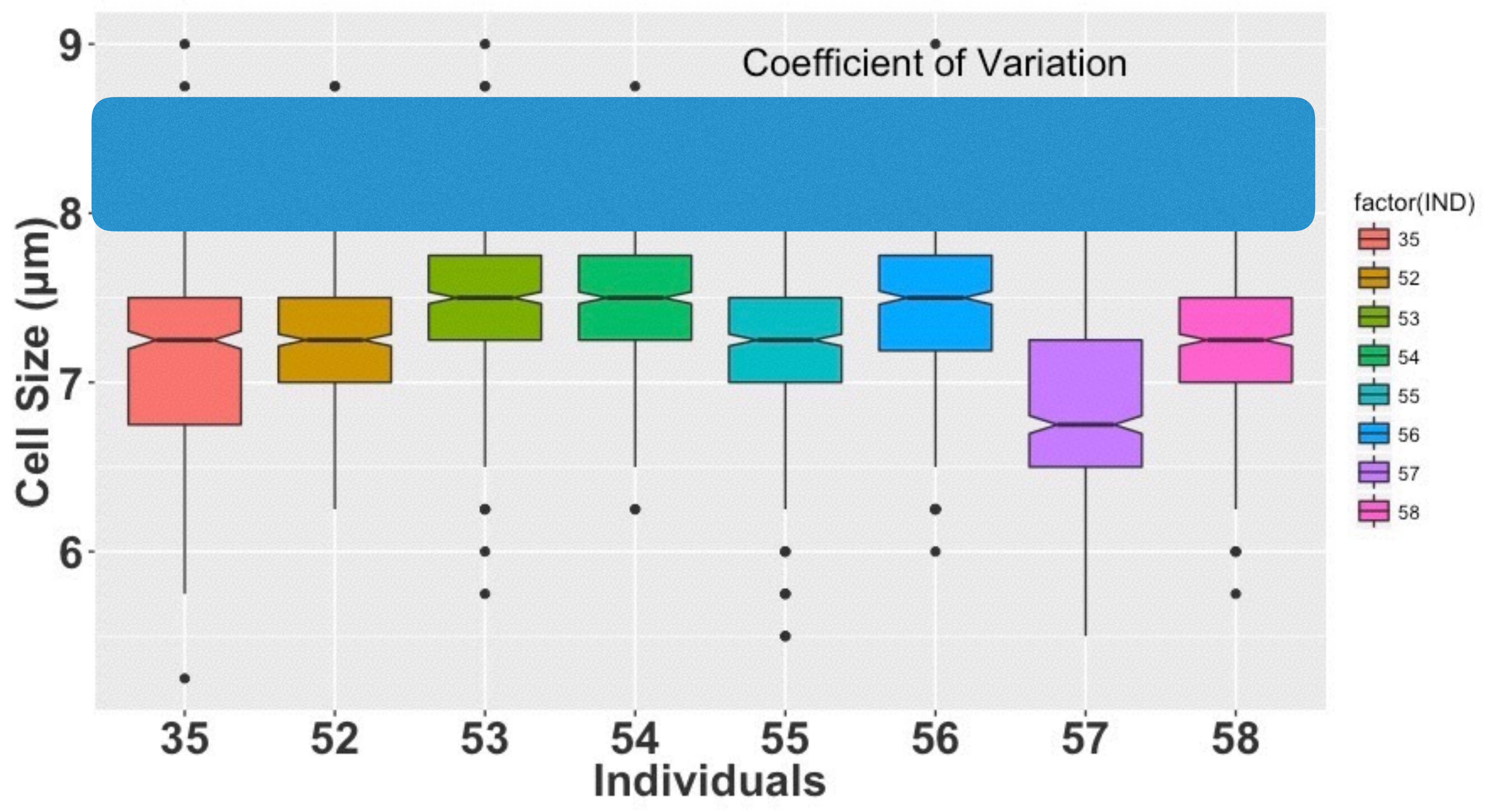
Coefficient of variation

Ind 52 = 0.0677
Ind 53 = 0.0628
Ind 54 = 0.0572
Ind 55 = 0.0605
Ind 56 = 0.0638
Ind 57 = 0.0604

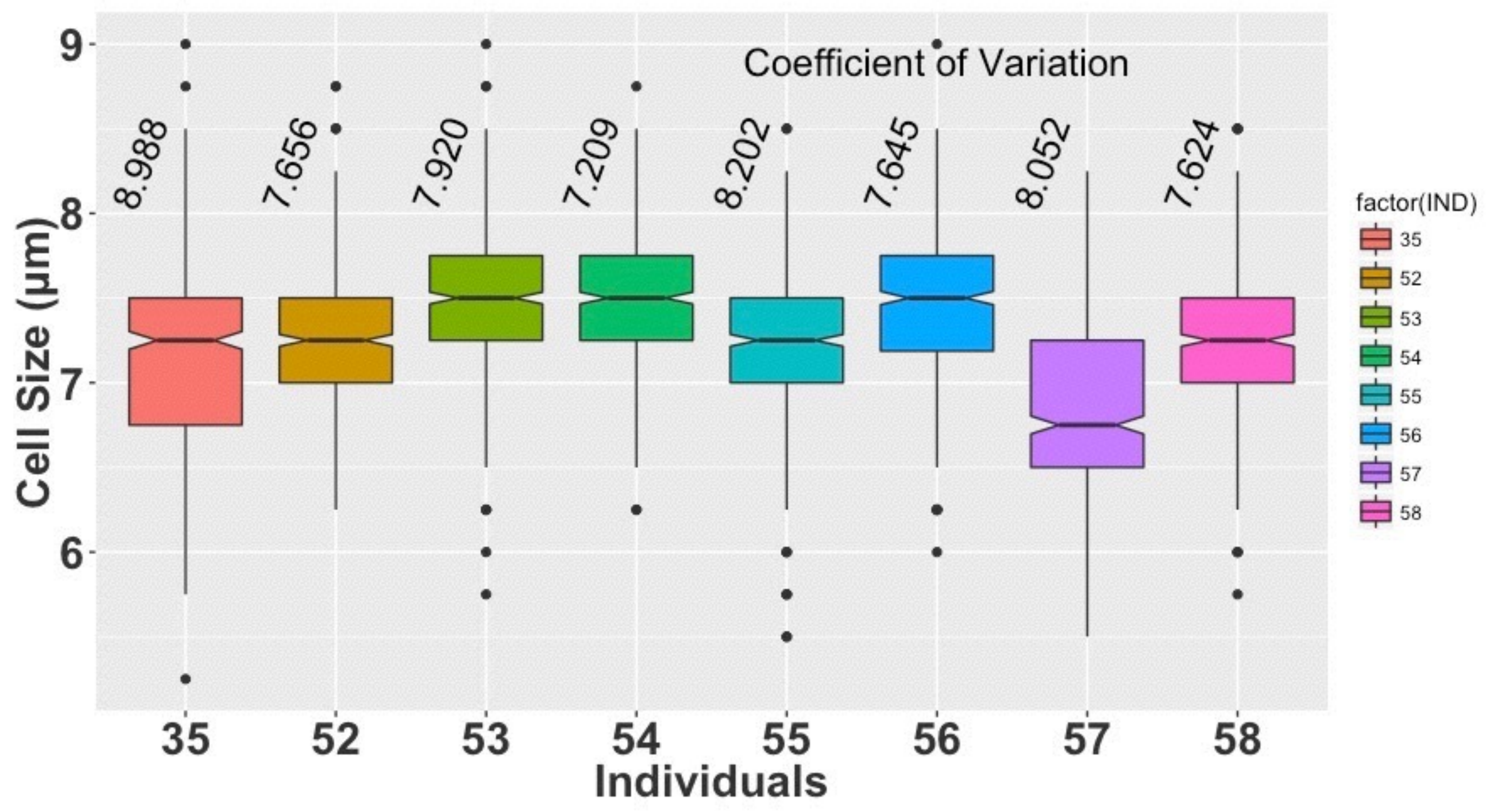


Mid points of class intervals μ.	Case 52 Sex M Age 20	53 M 36	54 M 27	55 M 34	56 M 20	57 M 20	58 M 21
4·75	...	...	...	...	...	...	...
5·00	...	...	...	...	...	...	...
5·25	...	...	...	...	...	...	...
5·50	...	...	...	2	...	1	...
5·75	...	1	...	3	...	2	1
6·00	...	1	...	3	1	20	3
6·25	9	3	2	17	5	53	5
6·50	17	10	10	29	14	78	21
6·75	50	42	28	70	37	99	46
7·00	82	65	61	101	68	111	80
7·25	145	105	120	119	123	84	142
7·50	82	100	127	85	93	36	97
7·75	60	93	77	42	85	11	52
8·00	33	43	40	19	47	4	36
8·25	17	26	23	8	22	1	13
8·50	3	8	11	2	4	...	4
8·75	2	2	1	...	...	...	...
9·00	...	1	...	...	1	...	...
9·25	...	...	...	...	...	...	...
9·50	...	...	...	...	...	...	...
Total	500	500	500	500	500	500	500
Mean diameter	7·313	7·438	7·449	7·162	7·405	6·850	7·302
Standard deviation	0·495	0·467	0·426	0·466	0·448	0·437	0·441
Variability per cent.	6·8	6·3	5·7	6·5	6·0	6·4	6·0

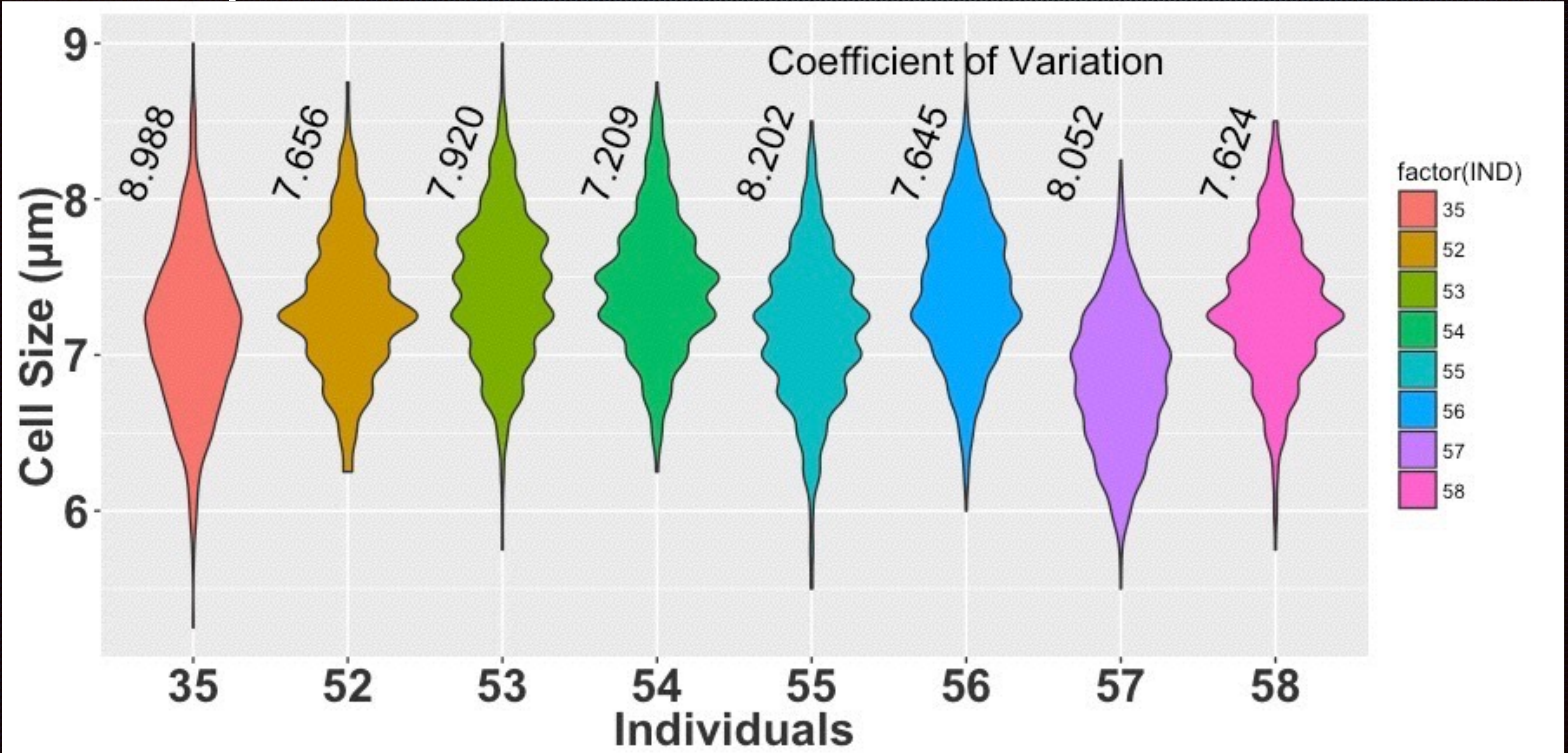
Box Plot of distribution of red blood cells in 8 healthy individuals

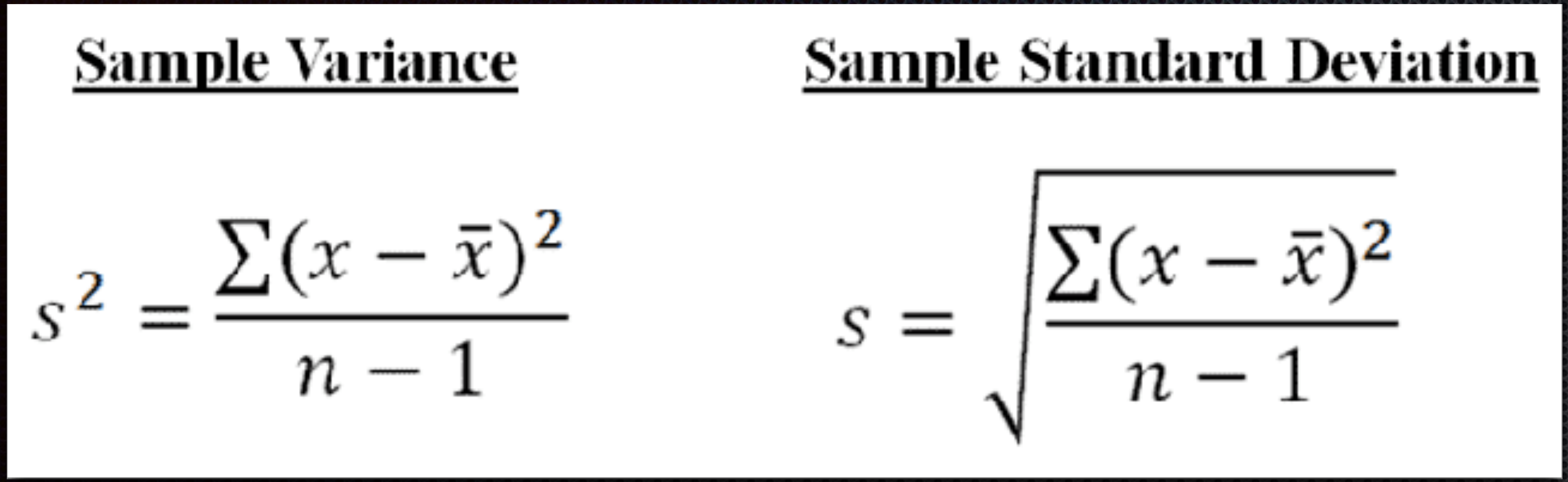


Box Plot of distribution of red blood cells in 8 healthy individuals



Violin Plot of distribution of red blood cells in 8 healthy individuals



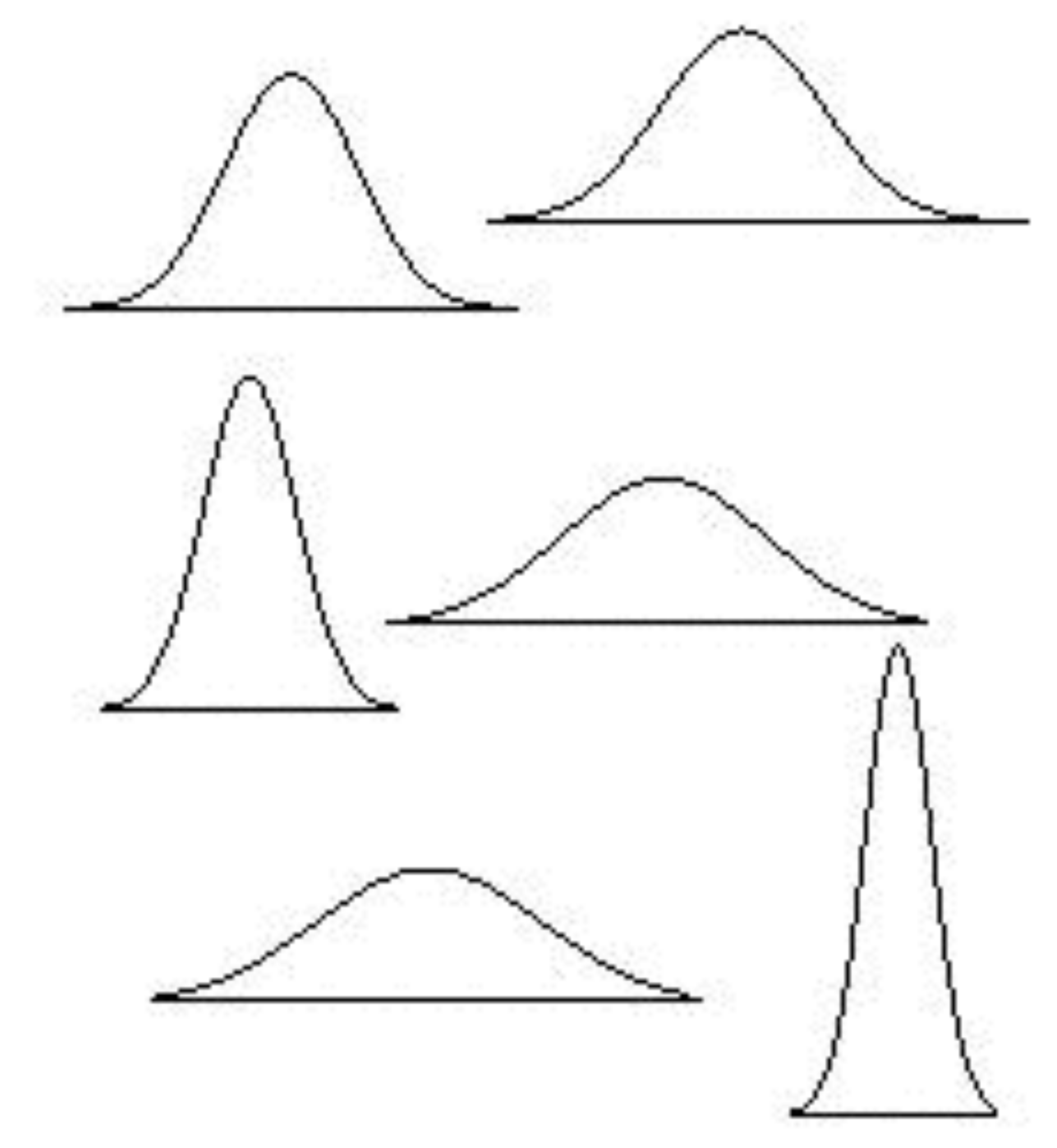


Sample Variance

$$s^2 = \frac{\sum(x-\bar{x})^2}{n-1}$$

Sample Standard Deviation

$$s = \sqrt{\frac{\sum(x-\bar{x})^2}{n-1}}$$



TESTS of homogeneity of variance and CV

A statistical interlude

Absolute variance

$$H_0: \sigma_1^2 = \sigma_2^2$$

$$F = \frac{s^2_{largest}}{s^2_{smallest}}$$

- NEVER use an F-test to test equality of variances
- Extremely sensitive to non-normality (even when a test of normality is not rejected)

Absolute variance

$$H_0\colon \sigma_1^2 = \sigma_2^2 \ldots \sigma_k^2$$

- NEVER use an Bartlett’s-test to test equality of variances (Rivest 1986)
- This is a generalization of the F test.
- Thus sensitive to non-normality

$$F = \frac{s^2_{largest}}{s^2_{smallest}}$$

Absolute variance

- Levene's Test
  - Deviation from the mean

$$y_i = |x_i - \overline{x}|$$

- Brown-Forsyth test
  - Deviation from the median

$$y_i = |x_i - x_{median}|$$

- Test on the Absolute deviation

Smith’s Test: Cedric A . B. Smith

The variance of
the estimation of
the variance

Grüneberg, H., G. S. Bains, R. J. Berry, L. Riles, C. A. B. Smith, and R. A. Weiss. "A Search for Genetic Effects of High Background Radioactivity. In: South India Special Report Series, 307." *Medical Research Council, London* (1966).

$$s^{2}_{s_j^{2}} = \frac{\sum (x_i - \overline{x})^4 - s_j^4\left(\frac{n-3}{n}\right)}{(n-2)(n-3)}$$

Described by Van Valen 2005

Smith’s Test

$$\chi^2_{k-1} = \sum \frac{s_j^4}{s^2_{s_j^2}} - \frac{\left[\sum \frac{s_j^2}{s^2_{s_j^2}}\right]^2}{\sum \frac{1}{s^2_{s_j^2}}}$$

Chi-Square statistics with (k-1) degree of freedom

Jackknifing (most robust approach)

- Jackknifing is a procedure where one element is removed from the data set and the calculations are preformed, until each element is removed one by one.
- Sample size must 20 or so.
- The only method to be able to calculate the CI of the

Relative Variation: Coefficient of Variation

$$CV = \frac{s}{\bar{x}} * 100$$

$$CV^{*} = (1 + \frac{1}{4n}) * CV$$

Unbiased estimate for small and medium sample size

Relative variance

- Levene’s Test for CV
    - Deviation from the mean

$$y_i = \frac{|x_i - \overline{x}|}{\overline{x}}$$

Smith's Test for CV

Substitute variables

$$s_{cv}^{2} \simeq \frac{cv^{2}}{2n}$$

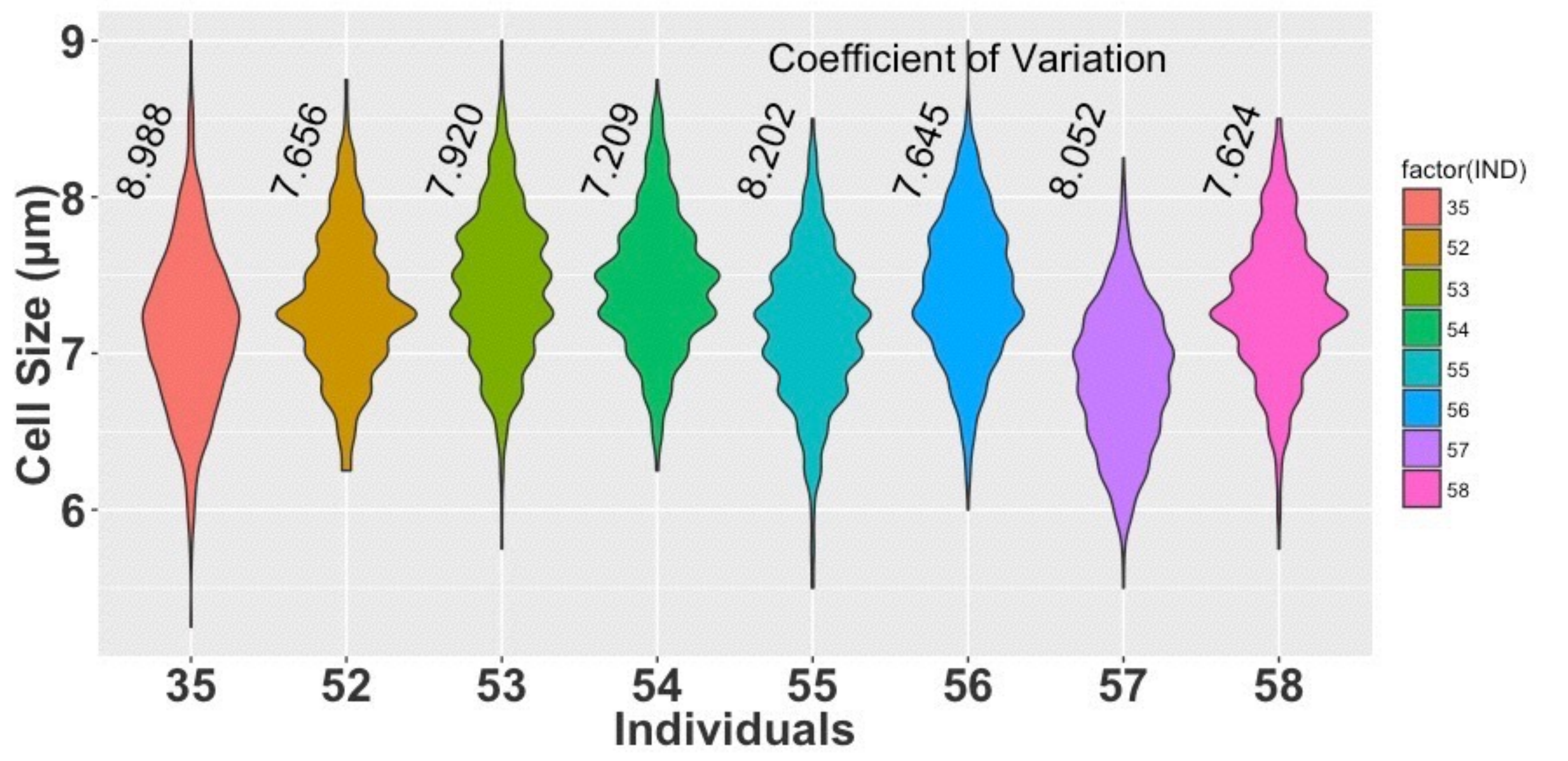
$$s_{cv}^{2} = s_{s_j^{2}}^{2} = \frac{\sum (x_i - \overline{x})^{4} - s_j^{4}\left(\frac{n-3}{n}\right)}{(n-2)(n-3)}$$

$$cv_j = s_j^{2}$$

$$\chi_{k-1}^{2} = \sum \frac{cv_j^{2}}{s_{cv}^{2}} - \frac{\left[\sum \frac{CV_j^{\square}}{s_{cv}^{2}}\right]^{2}}{\sum \frac{1}{s_{cv}^{2}}}$$

Chi-Square statistics with (k-1) degree of freedom

Are the CV’s significantly different?



R package: levene.test

Levene’s test of CV

```
levene.test(RBC2[,"CVmean"], RBC2[,"IND"], location="median", correction.method="zero.correction")
```

modified robust Brown-Forsythe Levene-type test based on the absolute deviations from the median with modified structural zero removal method and correction factor

Test Statistic = 2.423, p-value = 0.01782

Smith’s test of CV

$$\chi^2 = 25.77 \qquad \chi^2_{0.05,\ 7} = 14.07$$

Continuous variables: How common is Subindividual variation? Table 3.2 Herrera

Floral trait	Species	Number of plants	Number of flowers	Mean CV_{within}	References
Petal number	*Nyctanthes arbor-tristis*	17	82,173	9.8	Roy 1963
Flower length or diameter	*Castilleja* sp	10	20	7.1	L. Navarro
	Tabebuia chrysantha	10	30	9.0	J. M. Gómez
Corolla tube length	Lavandula latifolia	348	7262	3.2	Carlos Herrera

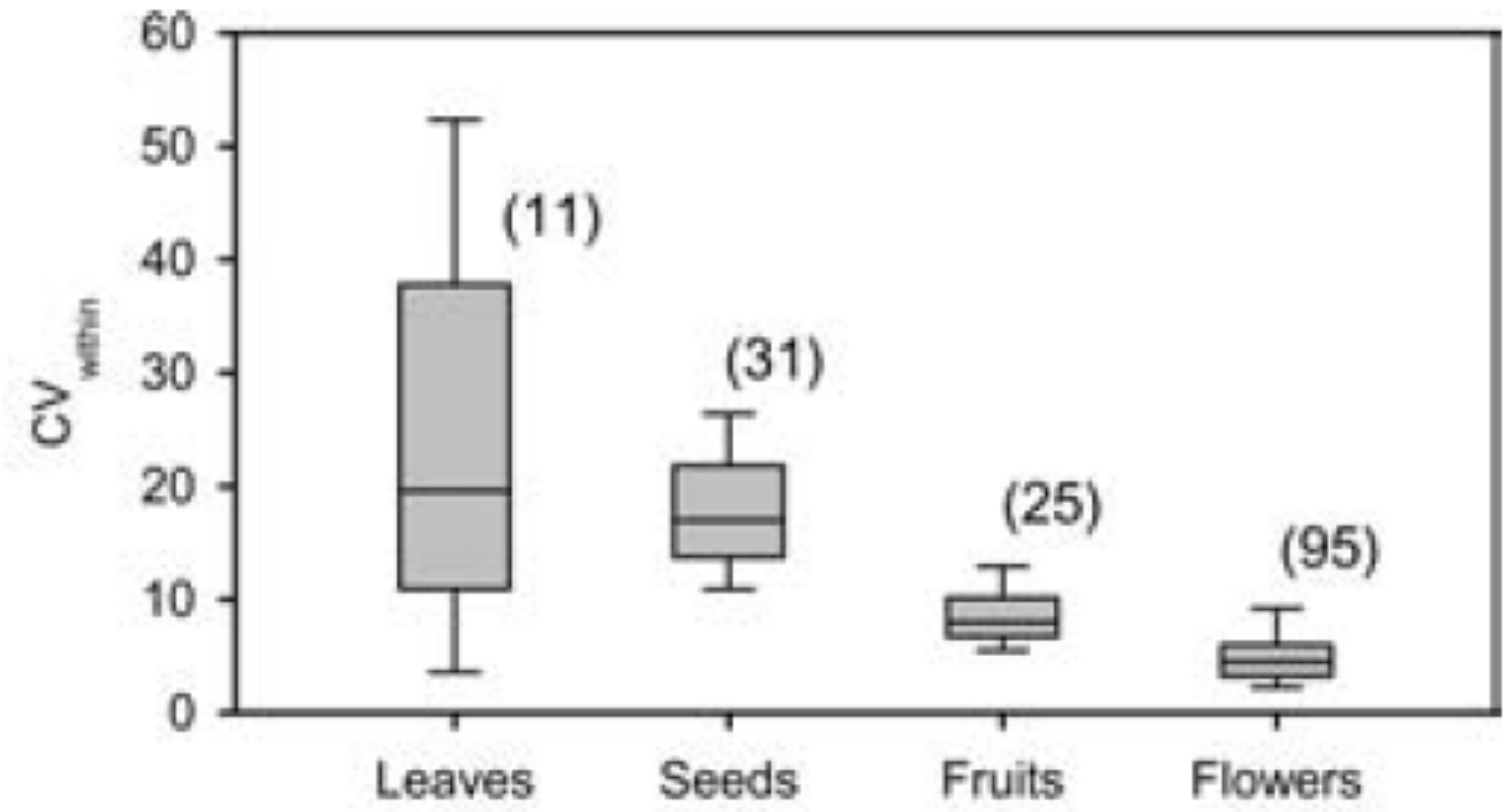
Range Mean CV: 1.7-16.3

>90% of data are from unpublished data

n= 95

General pattern of CV across plant characteristics

Figure 3.2 : Herrera 2009



Distribution of sub individual Variability in Time and Space

- Variation of reiterated structures organized along temporal, spatial and architectural axis

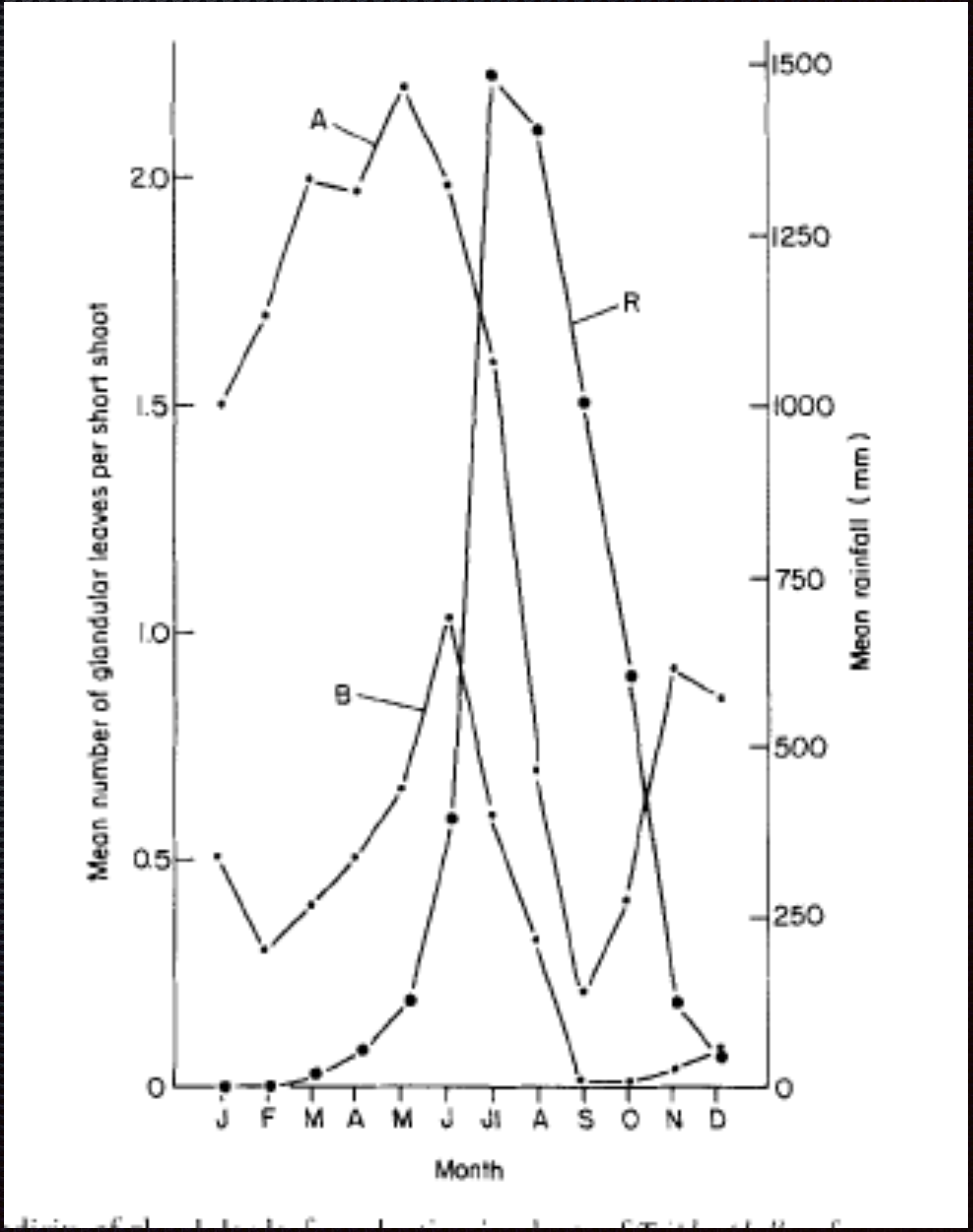
Time

- Simultaneous and sequential components of within-plant variation
    - Applies to individual plants over the same season or different years

Seasonal heterophylly

© Nicole Rebbert

GREEN, Sally., GREEN, T. L. and HESLOP-HARRISON, Y. (1979), Seasonal heterophylly and leaf gland features in *Triphyophyllum* (Dioncophyllaceae), a new carnivorous plant genus. Botanical Journal of the Linnean Society, 78: 99–116.



Decline in size of flower from early to late-opening flowers

Anemopsis macrophylla
Mimulus guttatus
Raphanus sativus
Solanum hirtum
etc.

Anemopsis macrophylla

Pellmyr 1987: Temporal patterns of ovule allocation, fruit set, and seed predation in*Anemonopsis macrophylla* (Ranunculaceae). Botanical Magazine, Tokyo

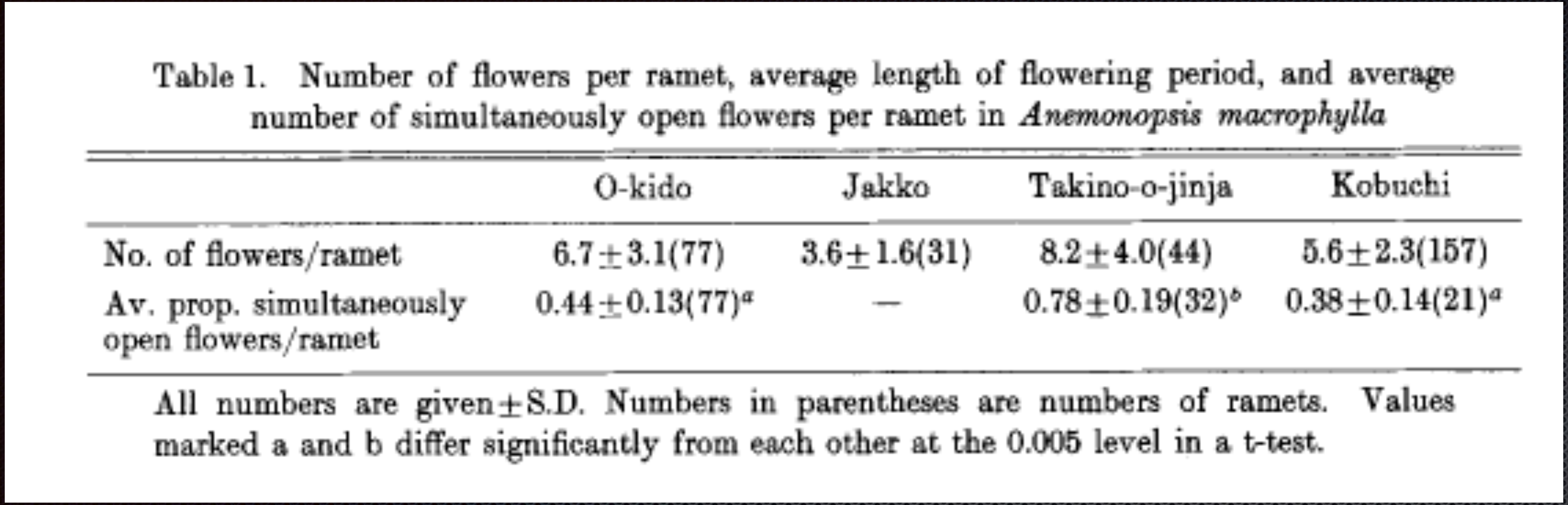
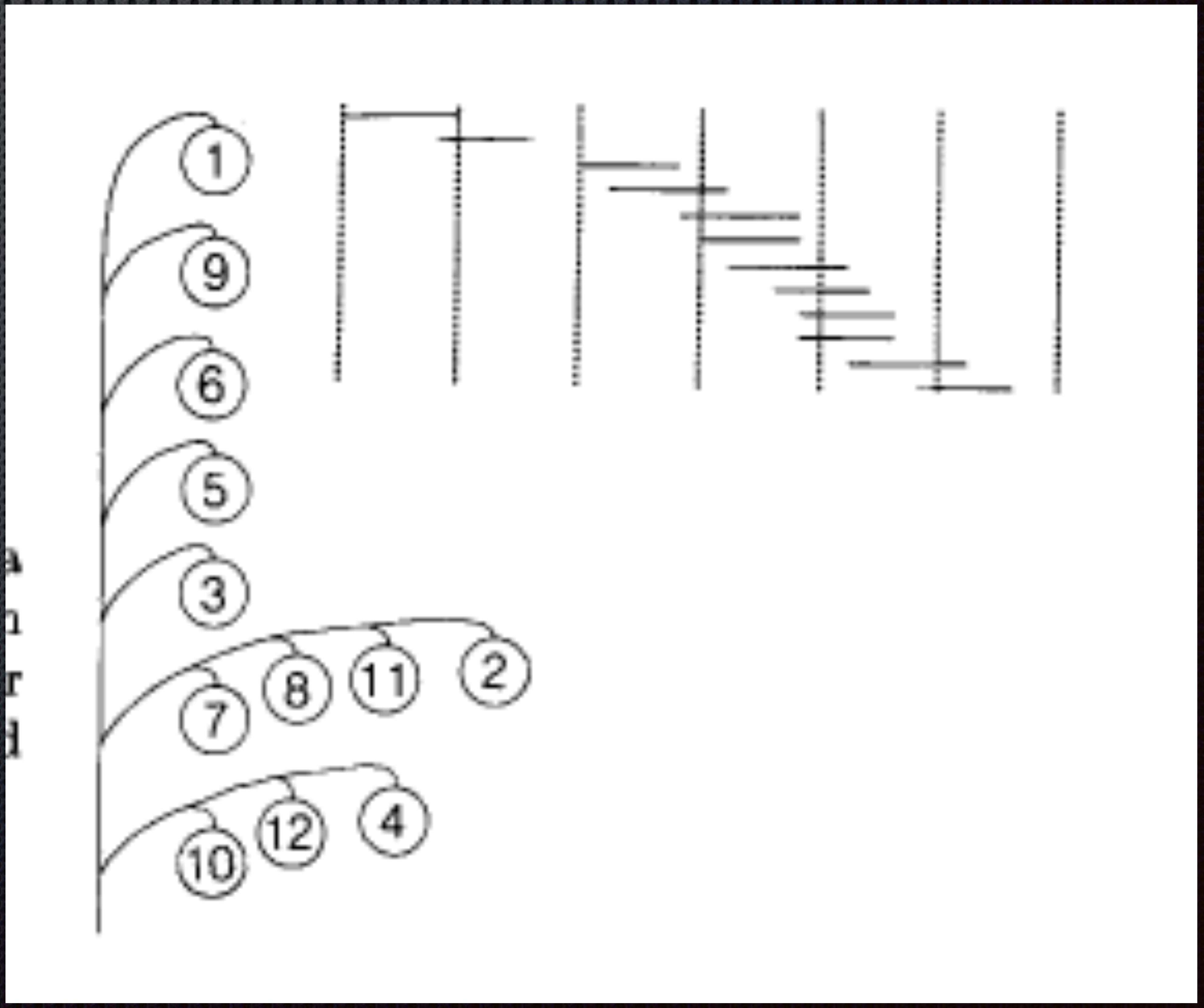


Table 1. Number of flowers per ramet, average length of flowering period, and average number of simultaneously open flowers per ramet in *Anemonopsis macrophylla*

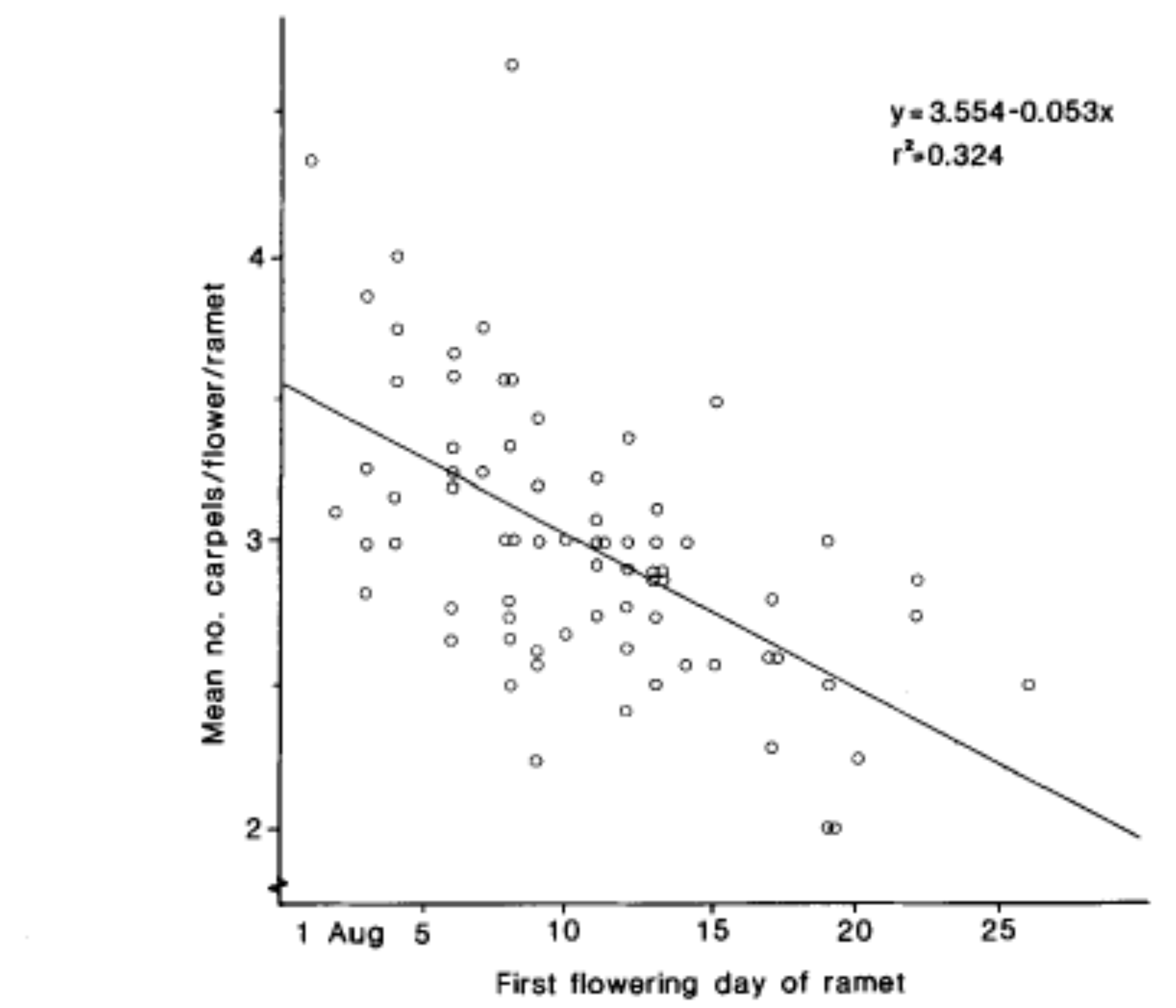
	O-kido	Jakko	Takino-o-jinja	Kobuchi
No. of flowers/ramet	6.7±3.1(77)	3.6±1.6(31)	8.2±4.0(44)	5.6±2.3(157)
Av. prop. simultaneously open flowers/ramet	0.44±0.13(77)[a]	—	0.78±0.19(32)[b]	0.38±0.14(21)[a]

All numbers are given±S.D. Numbers in parentheses are numbers of ramets. Values marked a and b differ significantly from each other at the 0.005 level in a t-test.

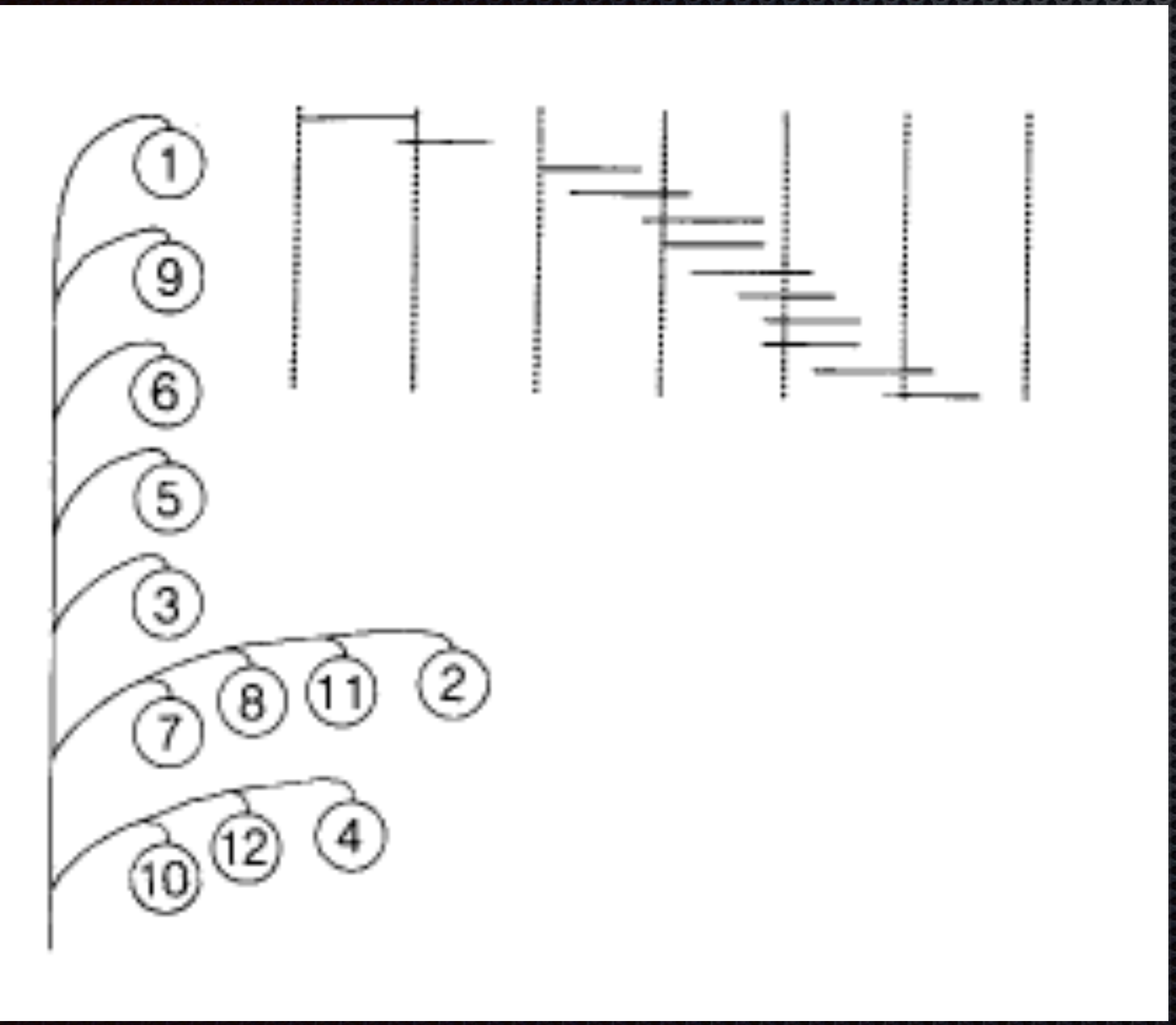
- Flowering sequence



Mean no. carpels/flower/ramet



Anemopsis macrophylla



Kang, H., & Primack, R. B.. (1991). Temporal Variation of Flower and Fruit Size in Relation to Seed Yield in Celandine Poppy (Chelidonium majus; Papaveraceae). *American Journal of Botany*, *78*(5), 711–722.

Variation as consequence in time

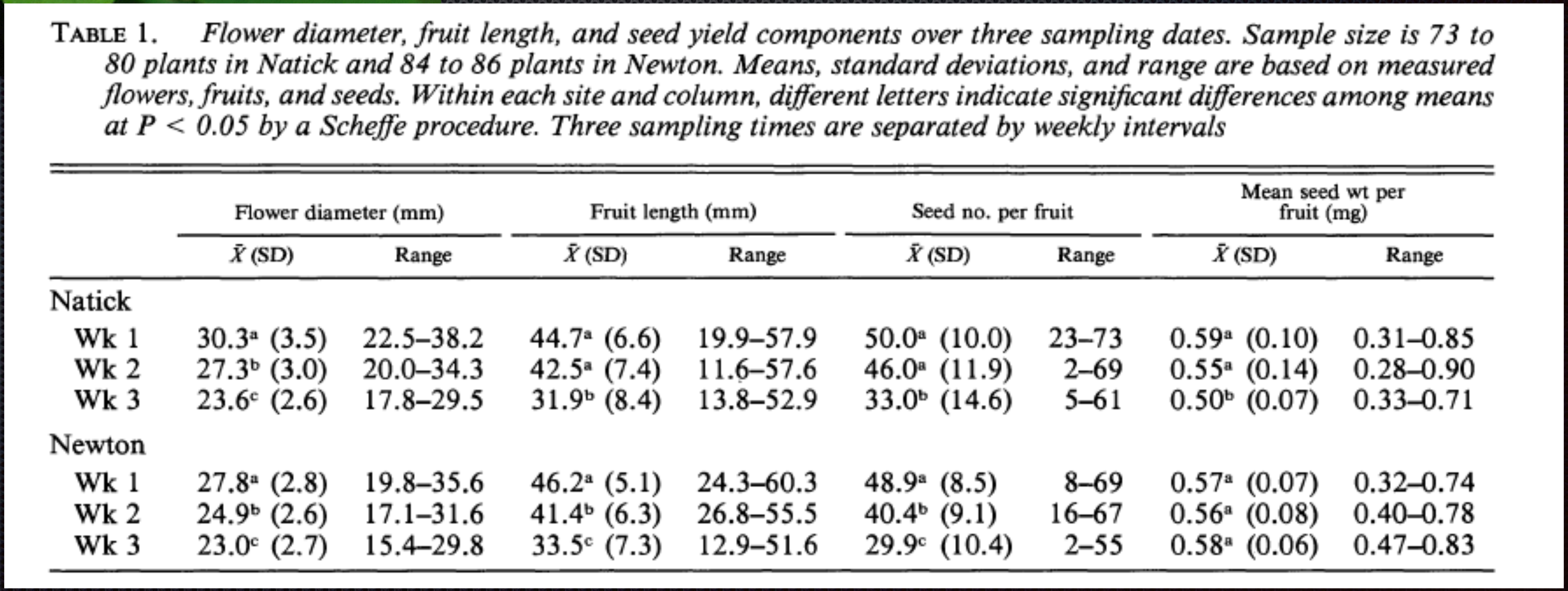


TABLE 1. *Flower diameter, fruit length, and seed yield components over three sampling dates. Sample size is 73 to 80 plants in Natick and 84 to 86 plants in Newton. Means, standard deviations, and range are based on measured flowers, fruits, and seeds. Within each site and column, different letters indicate significant differences among means at $P < 0.05$ by a Scheffe procedure. Three sampling times are separated by weekly intervals*

	Flower diameter (mm)		Fruit length (mm)		Seed no. per fruit		Mean seed wt per fruit (mg)	
	$\bar{X}$ (SD)	Range	$\bar{X}$ (SD)	Range	$\bar{X}$ (SD)	Range	$\bar{X}$ (SD)	Range
Natick								
Wk 1	30.3^{a} (3.5)	22.5–38.2	44.7^{a} (6.6)	19.9–57.9	50.0^{a} (10.0)	23–73	0.59^{a} (0.10)	0.31–0.85
Wk 2	27.3^{b} (3.0)	20.0–34.3	42.5^{a} (7.4)	11.6–57.6	46.0^{a} (11.9)	2–69	0.55^{a} (0.14)	0.28–0.90
Wk 3	23.6^{c} (2.6)	17.8–29.5	31.9^{b} (8.4)	13.8–52.9	33.0^{b} (14.6)	5–61	0.50^{b} (0.07)	0.33–0.71
Newton								
Wk 1	27.8^{a} (2.8)	19.8–35.6	46.2^{a} (5.1)	24.3–60.3	48.9^{a} (8.5)	8–69	0.57^{a} (0.07)	0.32–0.74
Wk 2	24.9^{b} (2.6)	17.1–31.6	41.4^{b} (6.3)	26.8–55.5	40.4^{b} (9.1)	16–67	0.56^{a} (0.08)	0.40–0.78
Wk 3	23.0^{c} (2.7)	15.4–29.8	33.5^{c} (7.3)	12.9–51.6	29.9^{c} (10.4)	2–55	0.58^{a} (0.06)	0.47–0.83

Flower length increase through the flowering season

Berry and Calvo 1991. Pollinator limitation and position dependent fruit set in the high Andean orchid *Myrosmodes cochleare* (*Orchidaceae*).
Plant Systematics and Evolution
Volume 174: 93-101

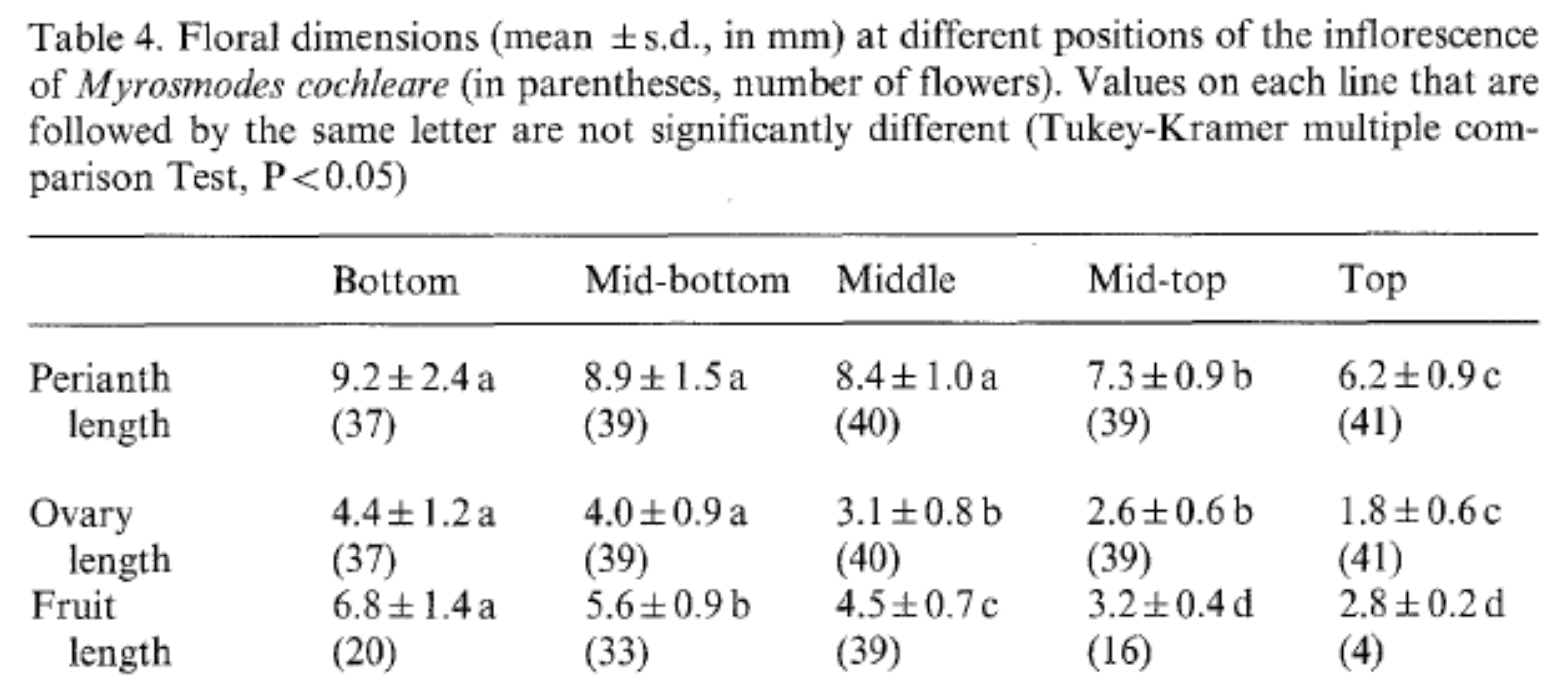


Table 4. Floral dimensions (mean ± s.d., in mm) at different positions of the inflorescence of *Myrosmodes cochleare* (in parentheses, number of flowers). Values on each line that are followed by the same letter are not significantly different (Tukey-Kramer multiple comparison Test, $P<0.05$)

	Bottom	Mid-bottom	Middle	Mid-top	Top
Perianth length	9.2 ± 2.4 a (37)	8.9 ± 1.5 a (39)	8.4 ± 1.0 a (40)	7.3 ± 0.9 b (39)	6.2 ± 0.9 c (41)
Ovary length	4.4 ± 1.2 a (37)	4.0 ± 0.9 a (39)	3.1 ± 0.8 b (40)	2.6 ± 0.6 b (39)	1.8 ± 0.6 c (41)
Fruit length	6.8 ± 1.4 a (20)	5.6 ± 0.9 b (33)	4.5 ± 0.7 c (39)	3.2 ± 0.4 d (16)	2.8 ± 0.2 d (4)

Lipid content variation in a season

Cedric O'Driscoll Worman and Colin A. Chapman (2005). Seasonal variation in the quality of a tropical ripe fruit and the response of three frugivores. Journal of Tropical Ecology, 21, pp 689-697. doi:10.1017/S0266467405002725.

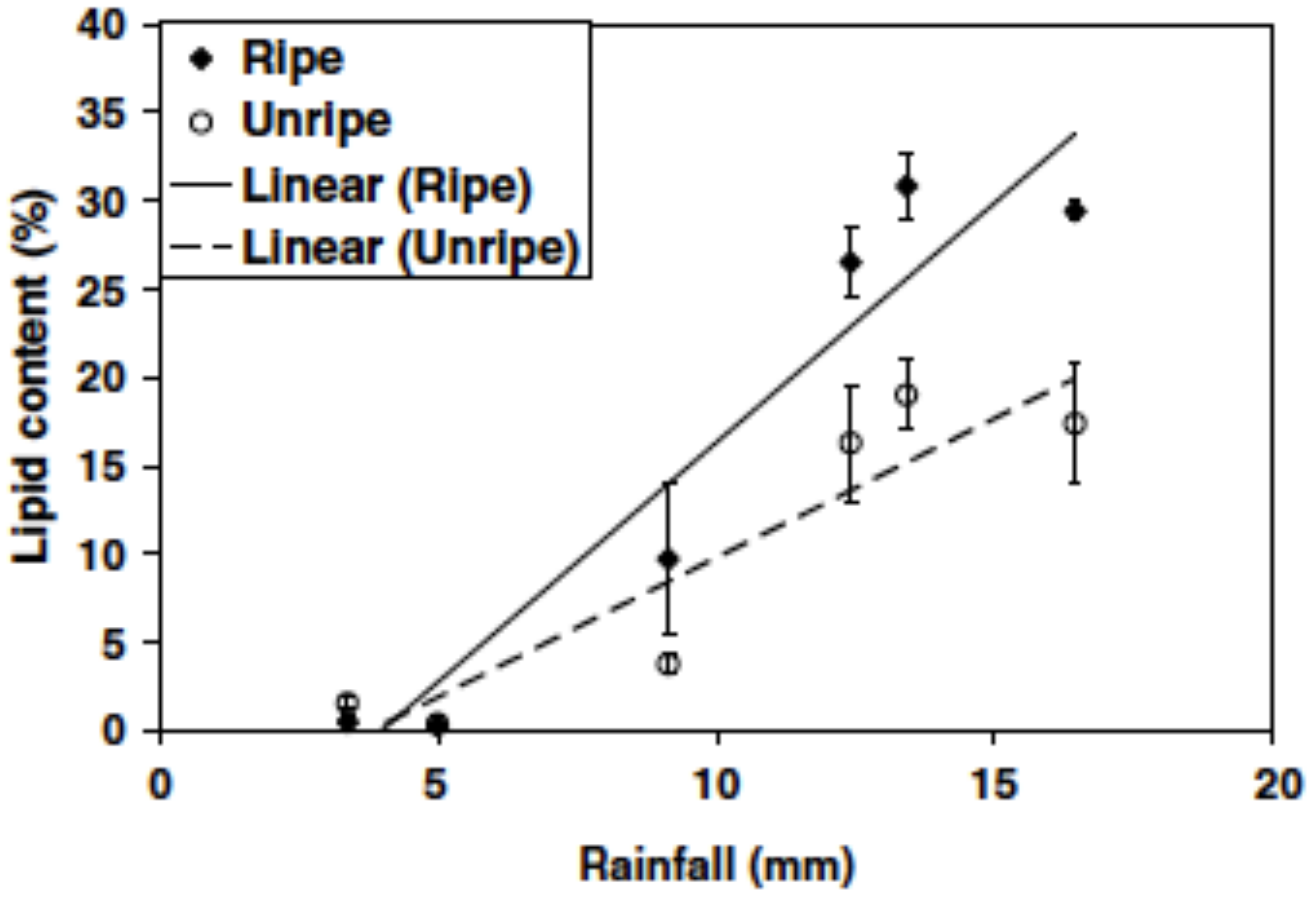


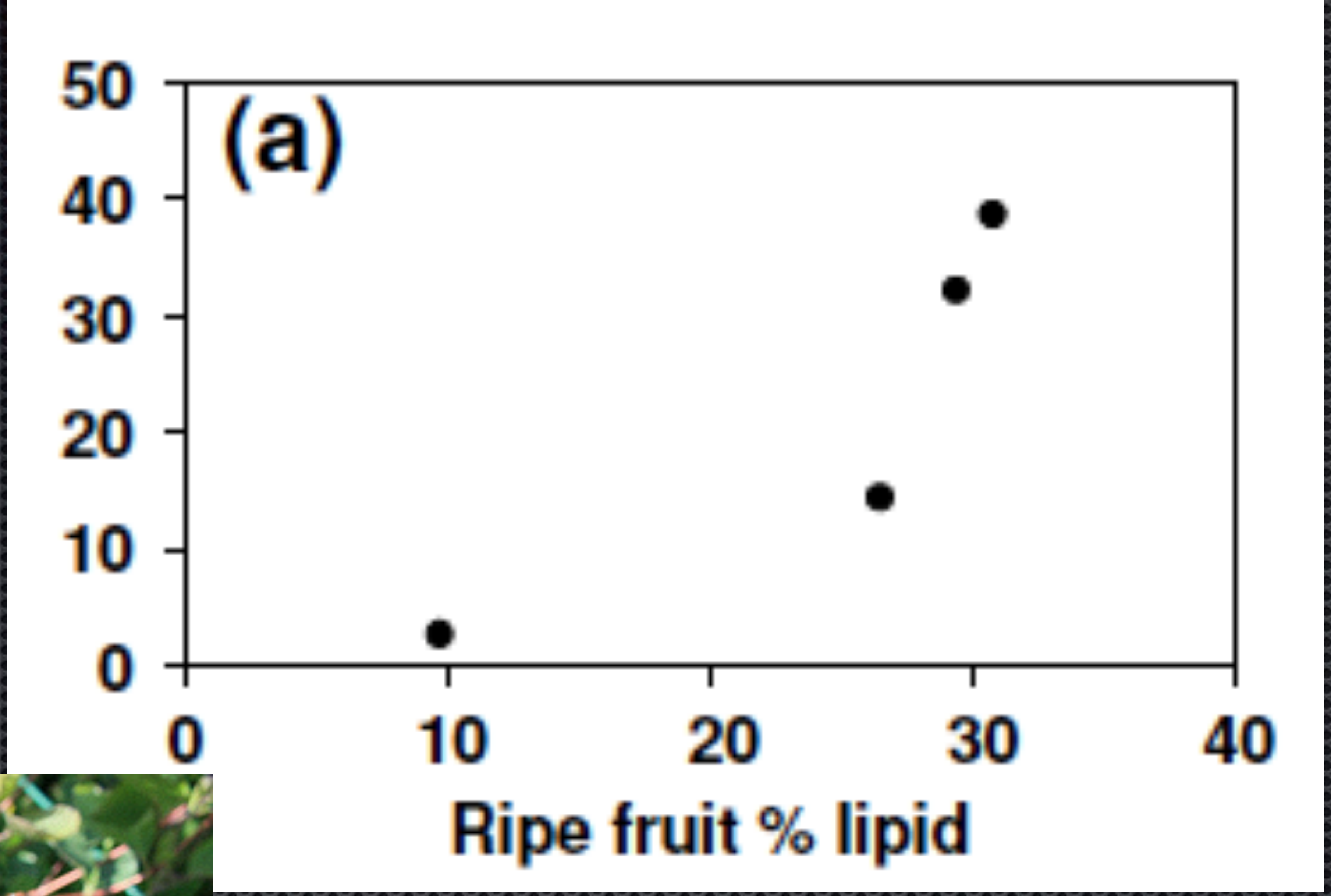
Figure 1. The relationship between the monthly dry matter lipid content of ripe and unripe *Celtis durandii* fruit and the summed daily rainfalls of the concurrent and previous months at Kibale National Park, Uganda for June 2002–November 2002 (ripe: $y = 0.0271x - 0.108$, $r^2 = 0.91$, $n = 6$, $P = 0.003$; unripe: $y = 0.0158x - 0.0596$, $r^2 = 0.85$, $n = 6$, $P = 0.009$). The error bars represent ± 1 SE.

Cannabaceae:
Uganda

Celtic durandii

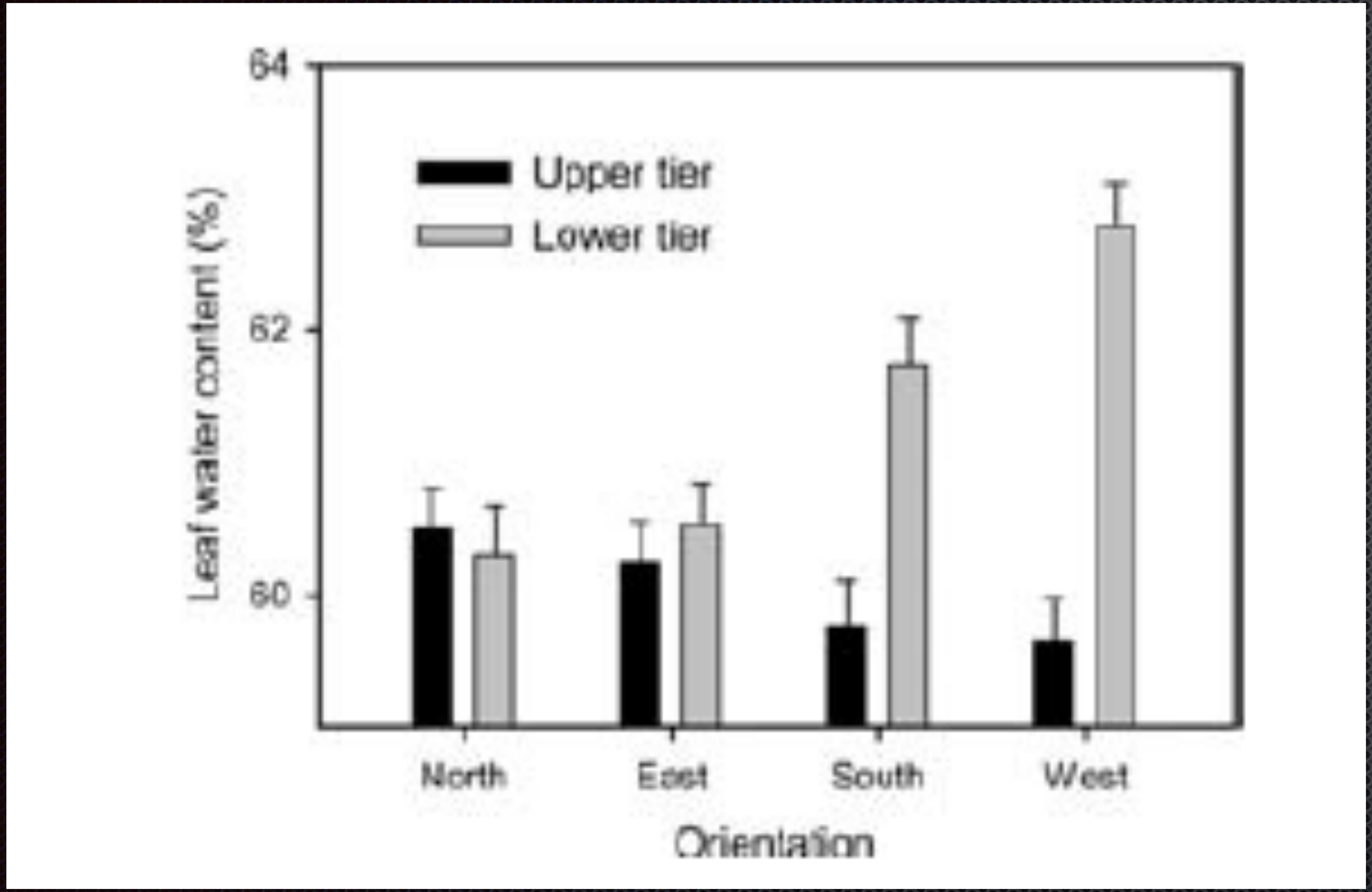
Cercopithecus mitis

- % fruit in diet



Spatial Distribution

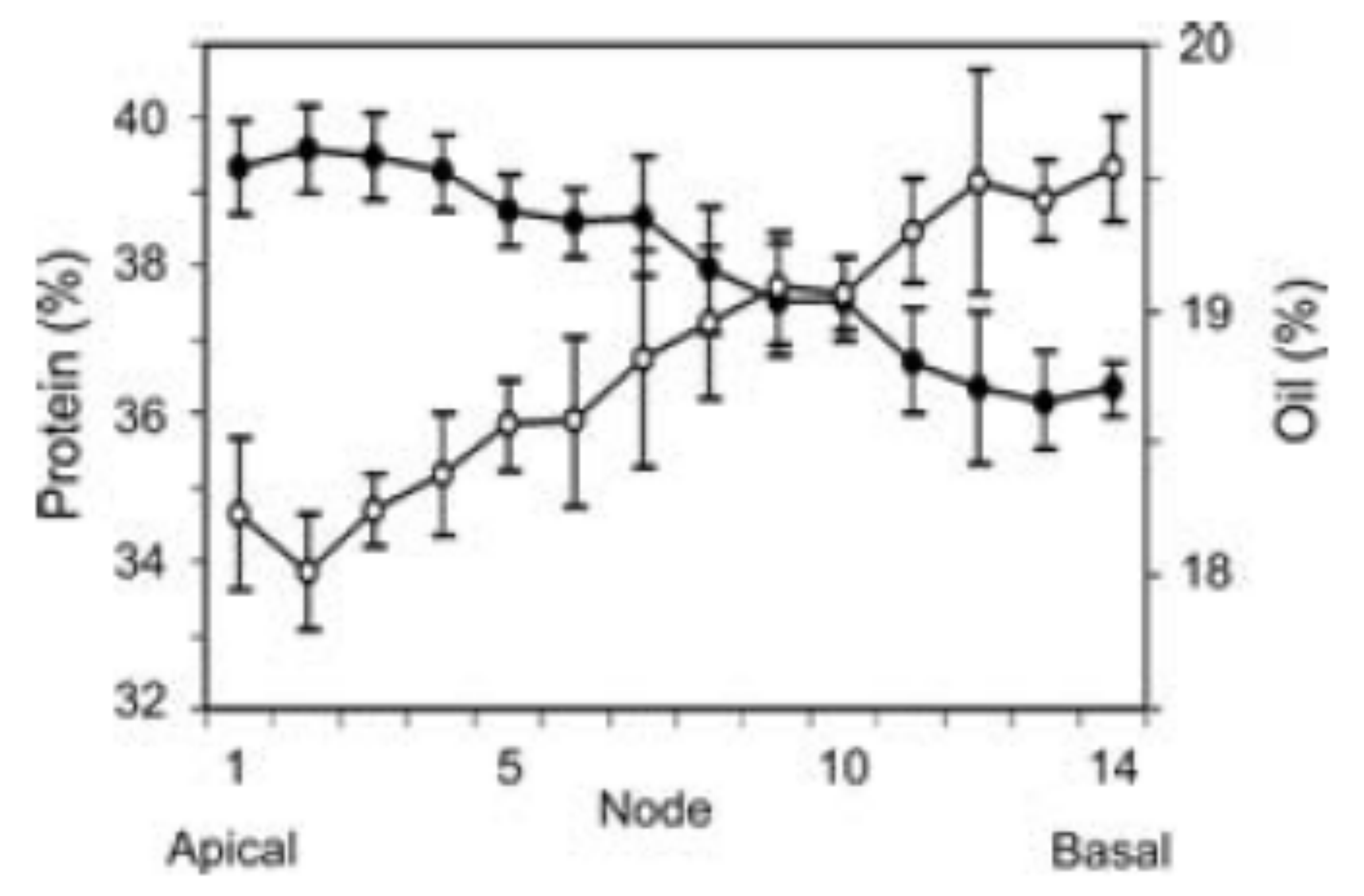
Spatial Distribution: Alonso 1997a unpublished: *Prunus mahaleb*



Prunes

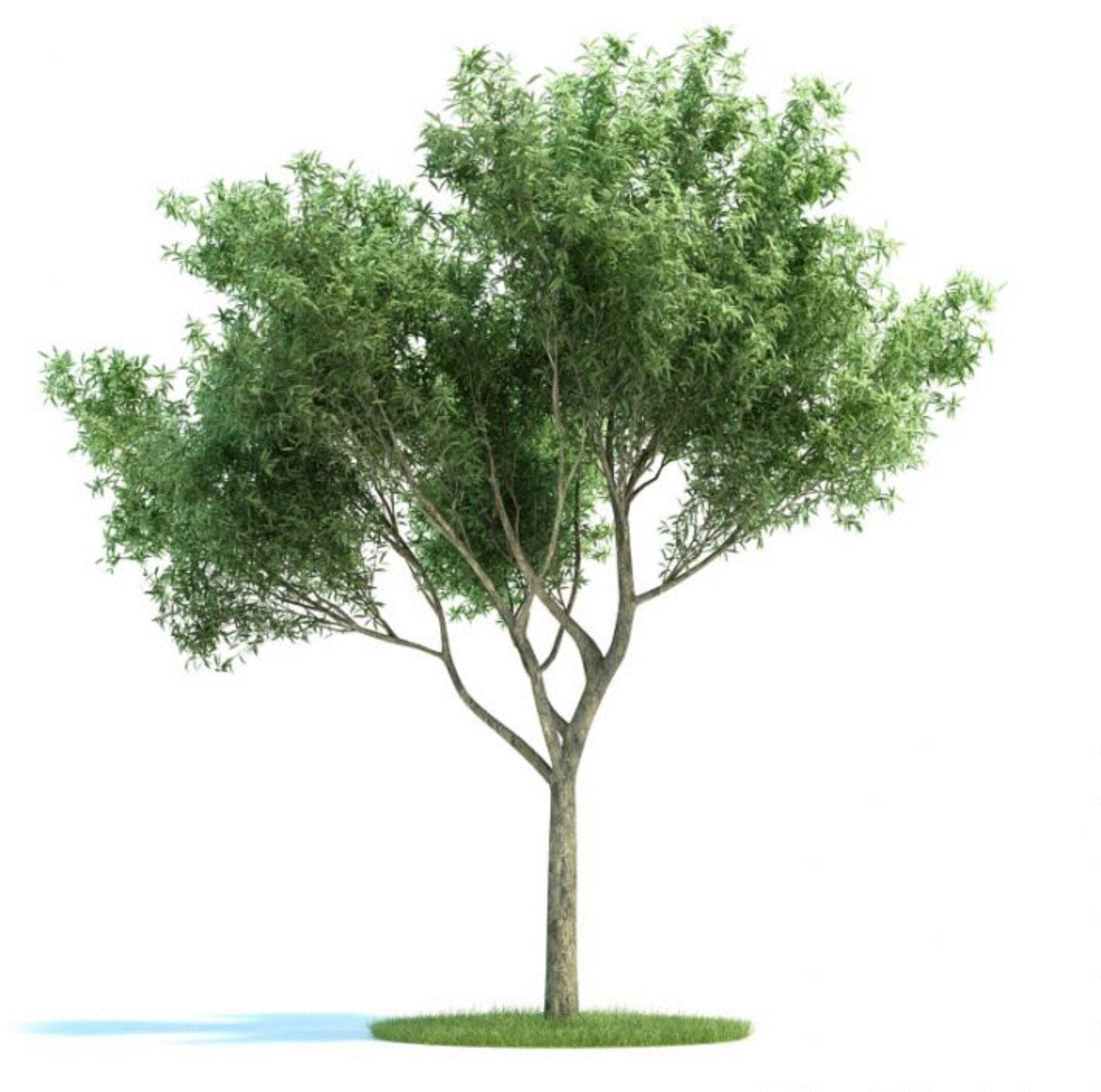
Protein and Oil content in Soybean (*Glycine max*) as function of node position

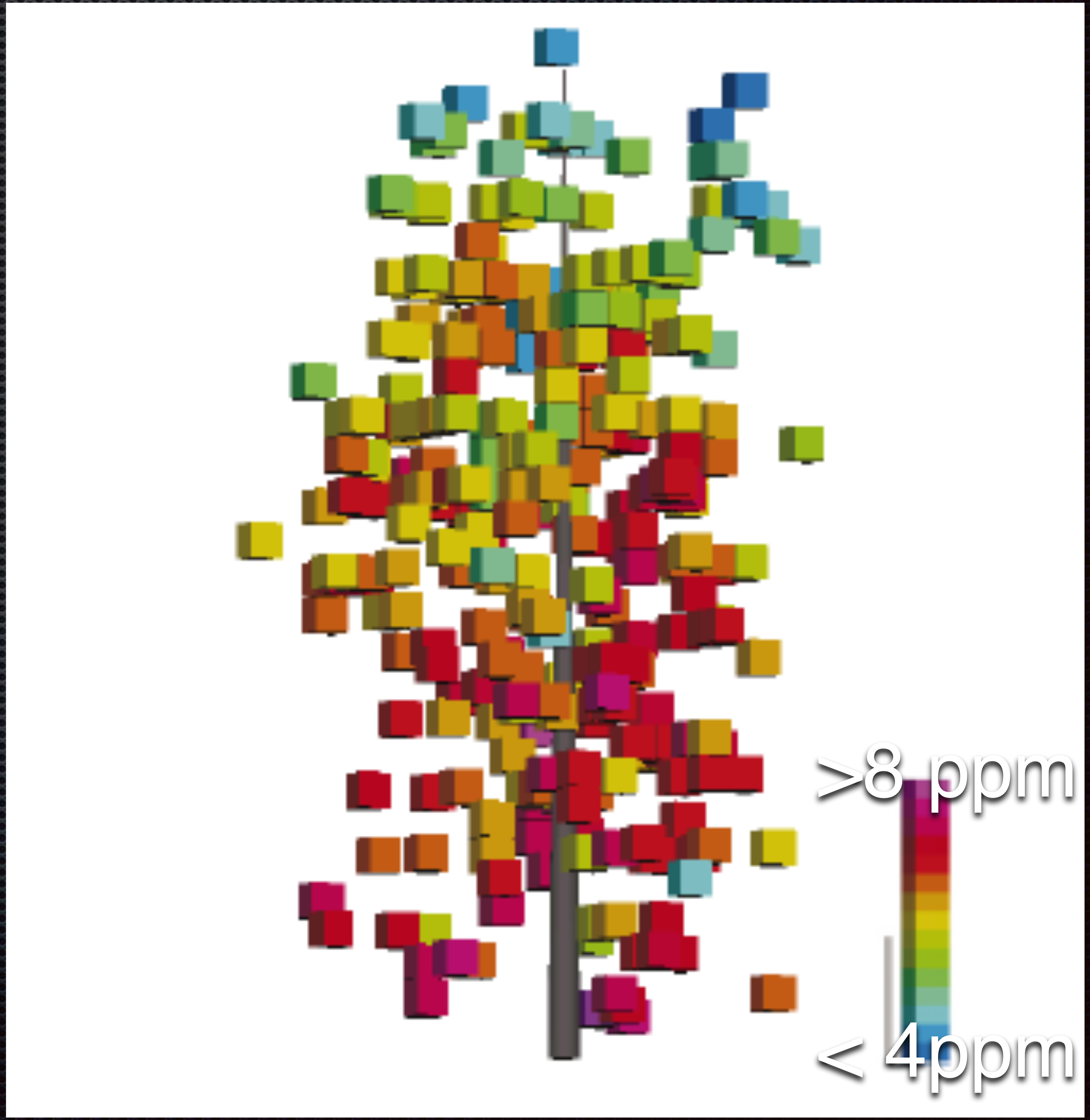
Bennett, John O., et al. "Positional effect on protein and oil content and composition of soybeans." *Journal of agricultural and food chemistry* 51.23 (2003): 6882-6886.



Spatial Distribution in 3D

Luyssaert, Sebastiaan, M. Van Meirvenne, and Noël Lust. "Cadmium variability in leaves of a *Salix fragilis*: simulation and implications for leaf sampling." *Canadian journal of forest research* 31.2 (2001): 313-321.





Causes of Sub-individual variation?

- What are the cause of sub-individual variation?
  - Genetic heterogeneity
  - Semi-autonomous, programmed responses of organs within an individual to environmental cues: Developmental phenotypic plasticity

Arabidopsis thaliana

Genetic Mosaic

- 94 different genes are known to yield mutations causing abnormal leaf morphologies in *Aribidopsis*
- a dozen of quantitative trait loci (QTL) control quantitative variation in leaf, flowers and seed features

Organ-Level Developmental Plasticity

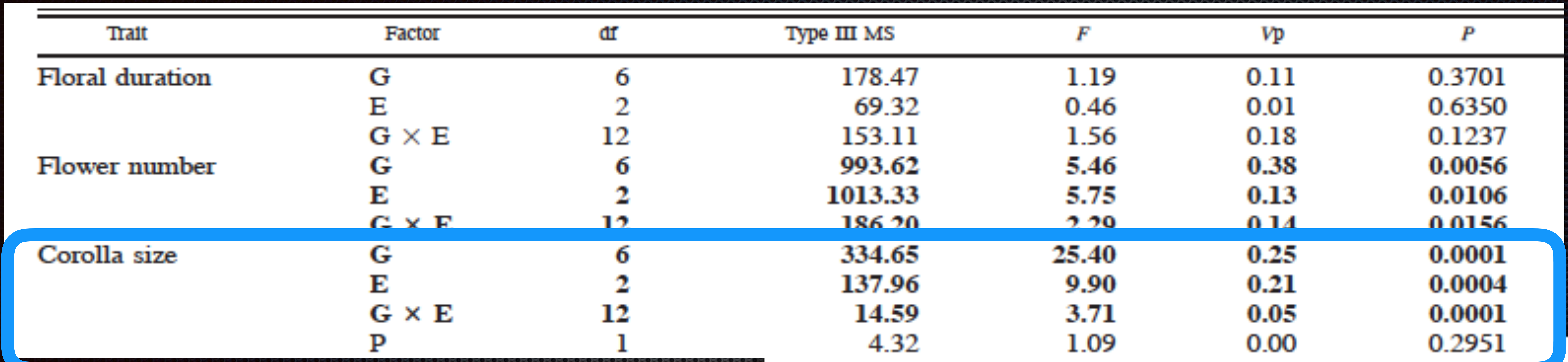
- Phenotypic constancy is not a cue for the absence of genetic variation
- nor does phenotypic variation inevitably require genetic differences

Table 5.1 Organ-level phenotypic plasticity, in which variation in some external environmental factor induces predictable phenotypic responses at the level of individual organs

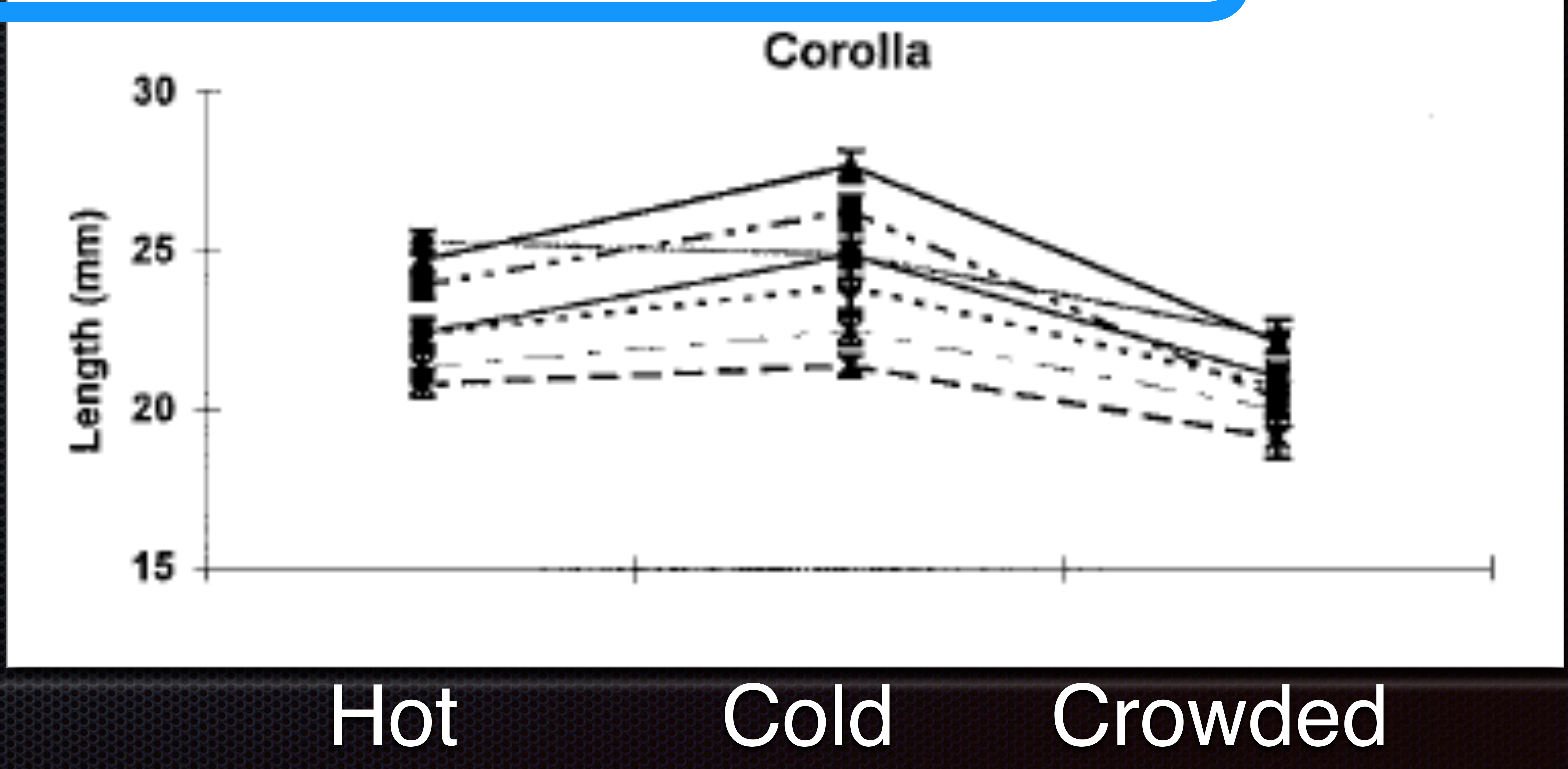
Herrera 2009

- *Callitriche heterophylla*
- Environmental cue
  - Submergence in water
  - Form of leaf: ovate vs.linear

Temperature effect on Corolla size



Trait	Factor	df	Type III MS	*F*	*V*p	*P*
Floral duration	G	6	178.47	1.19	0.11	0.3701
	E	2	69.32	0.46	0.01	0.6350
	G × E	12	153.11	1.56	0.18	0.1237
Flower number	G	6	993.62	5.46	0.38	0.0056
	E	2	1013.33	5.75	0.13	0.0106
	G × E	12	186.20	2.29	0.14	0.0156
Corolla size	G	6	334.65	25.40	0.25	0.0001
	E	2	137.96	9.90	0.21	0.0004
	G × E	12	14.59	3.71	0.05	0.0001
	P	1	4.32	1.09	0.00	0.2951



Vogler, Donna W., Shani Peretz, and Andrew G. Stephenson. "Floral plasticity in an iteroparous plant: the interactive effects of genotype, environment, and ontogeny in Campanula rapunculoides (Campanulaceae)." *American Journal of Botany* 86.4 (1999): 482-494.

Haldane-Roy conjecture?

Subindividual Variability as an Individual Property:

Individual plants have not only their characteristic means, but also their characteristic standard deviations and characteristic spatial patterns of within-plant variation.

Arquitectural Variation

Table 7.1: Variation among conspecific individuals in the magnitude of within-plant for leaf, flower, fruit and sedd traits. (Carlos Herrera: Multiplicity in Unity, 2009)

Within Plant Variation (CVwithin)

Trait	Species	Range	Interquartile range	Significance of Ind differences
Leaf area	*Daphne gnidium*	12.7-26.9	7.3	****
	Prunus mahaleb	37.9-77.9	12.2	****
Longevity Leaf	Thuja plicat	12.1-37.3	10.2	ns
Water content	Daphne laureola	1.0-9.5	1.5	****
Number of teeth on margin	Nyctanthes arbortritis	54.1-258.9	147.8	na

Within Plant Variation (CVwithin)

Trait	Species	Range	Interquartile range	Significance of Ind differences
Spur length	*Viola cazorlensis*	1.2-26.7	6.5	****
Corolla length	*Daphne laurel*	6.5-23.7	4.1	*
Fruit diameter	*Ipomoea wolcottiana*	3.1-31.9	7.3	****
	Rosa canina	4.8-35.4	3.2	*
	Arum italicum	4.1-13.0	2.8	ns
Fruit mass	*Hedera helix*	23.7-34.9	2.1	*
Elaiosome mass	*Helleborus foetidus*	6.0-51.1	9.1	****

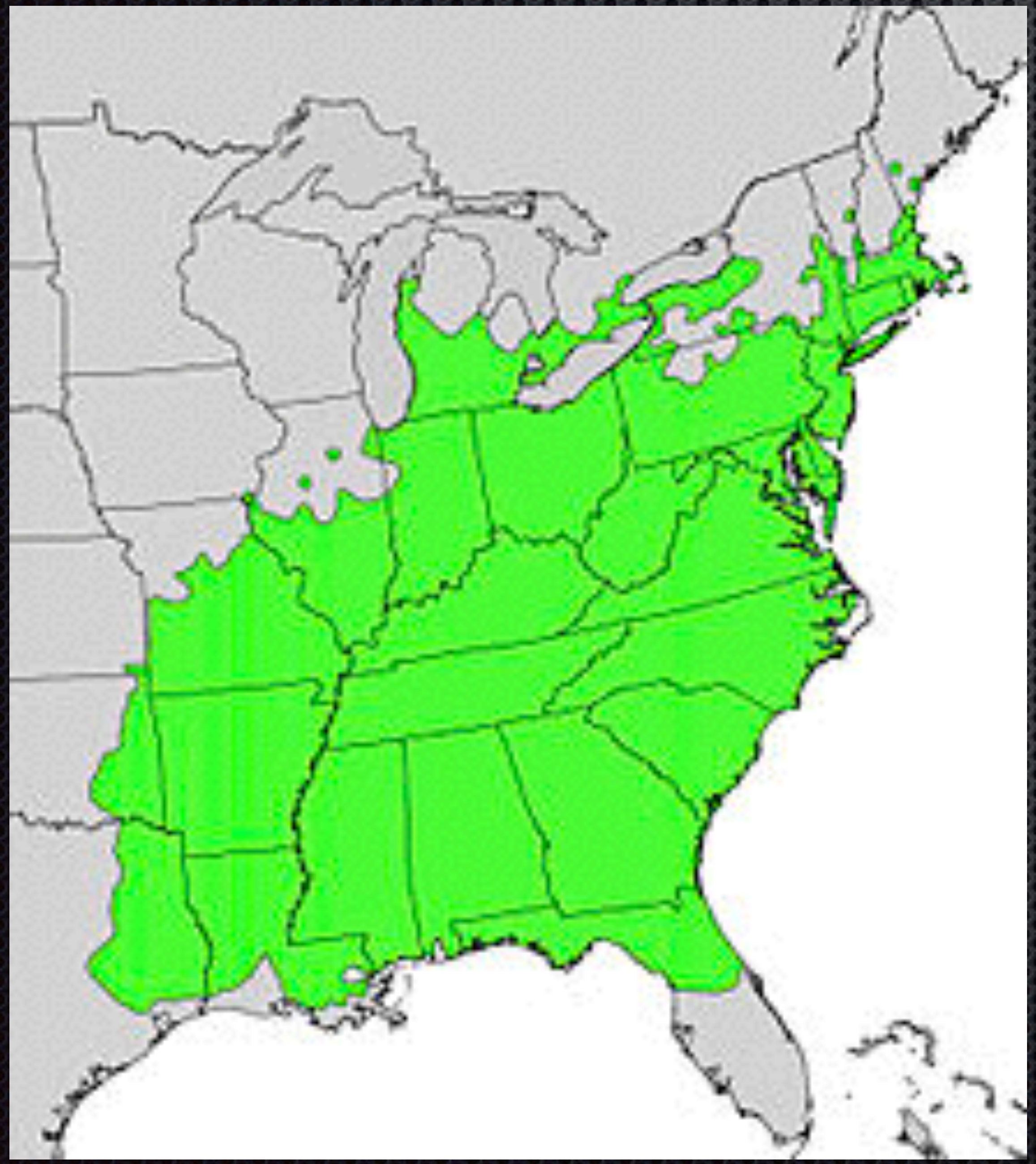
Literature review Herrera 2009

- Table 7.1:
- Out of 62 tests only 10 were non significant
  - Leaf Area
  - Fresh Mass
  - Length
  - Longevity
  - Number of teeth
  - Water content
  - Leaf width
  - Petal number
  - Petal length
  - Corolla length or diameter
  - Spur length
  - Nectar production
  - Fruit diameter
  - Fruit mass
  - Seed Mass

Individual Differences in the organization of within-plant Variation

- *Sassafras albidum*

- *Chlorophyll content*

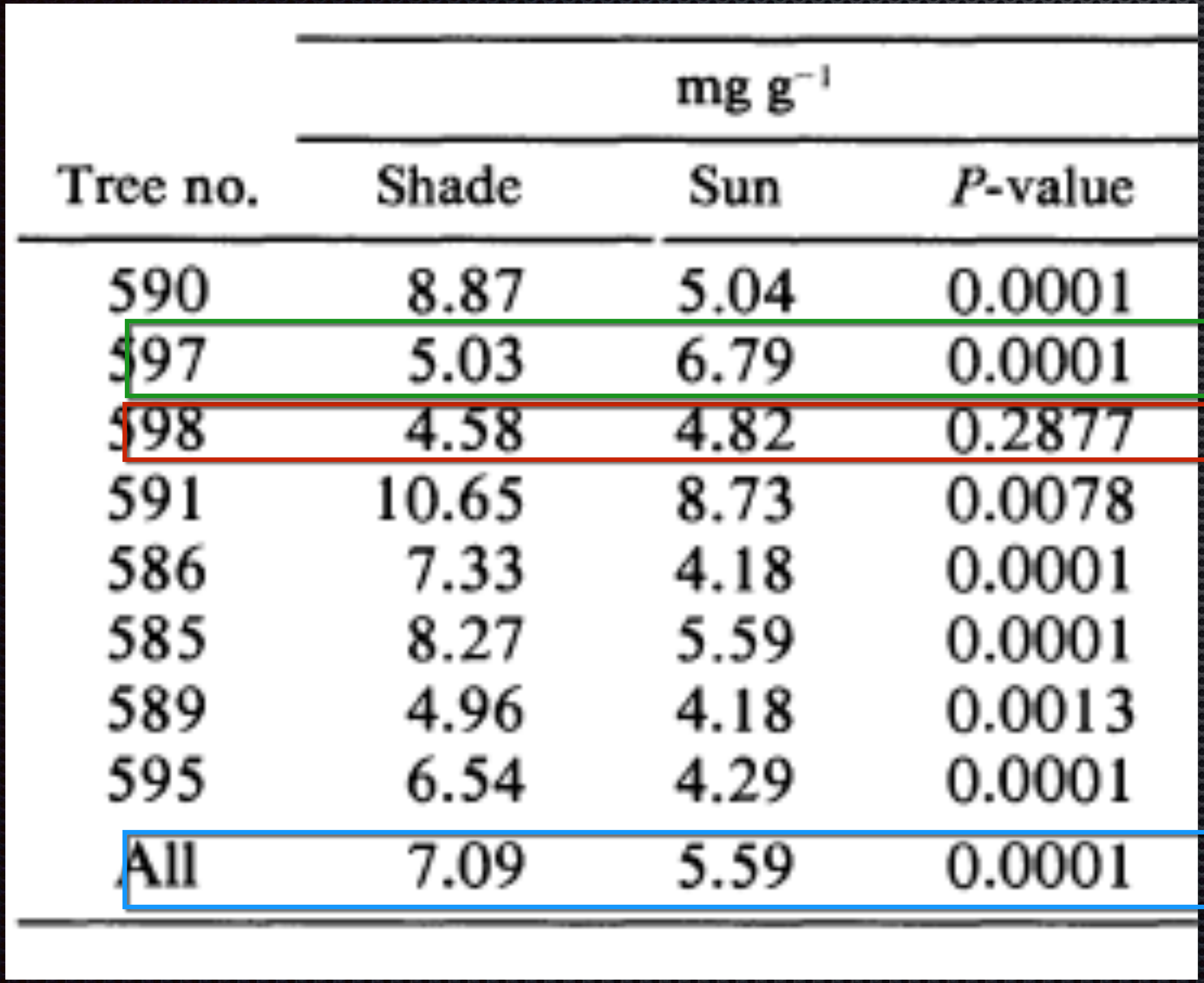


De Soyza *et al.* 1990

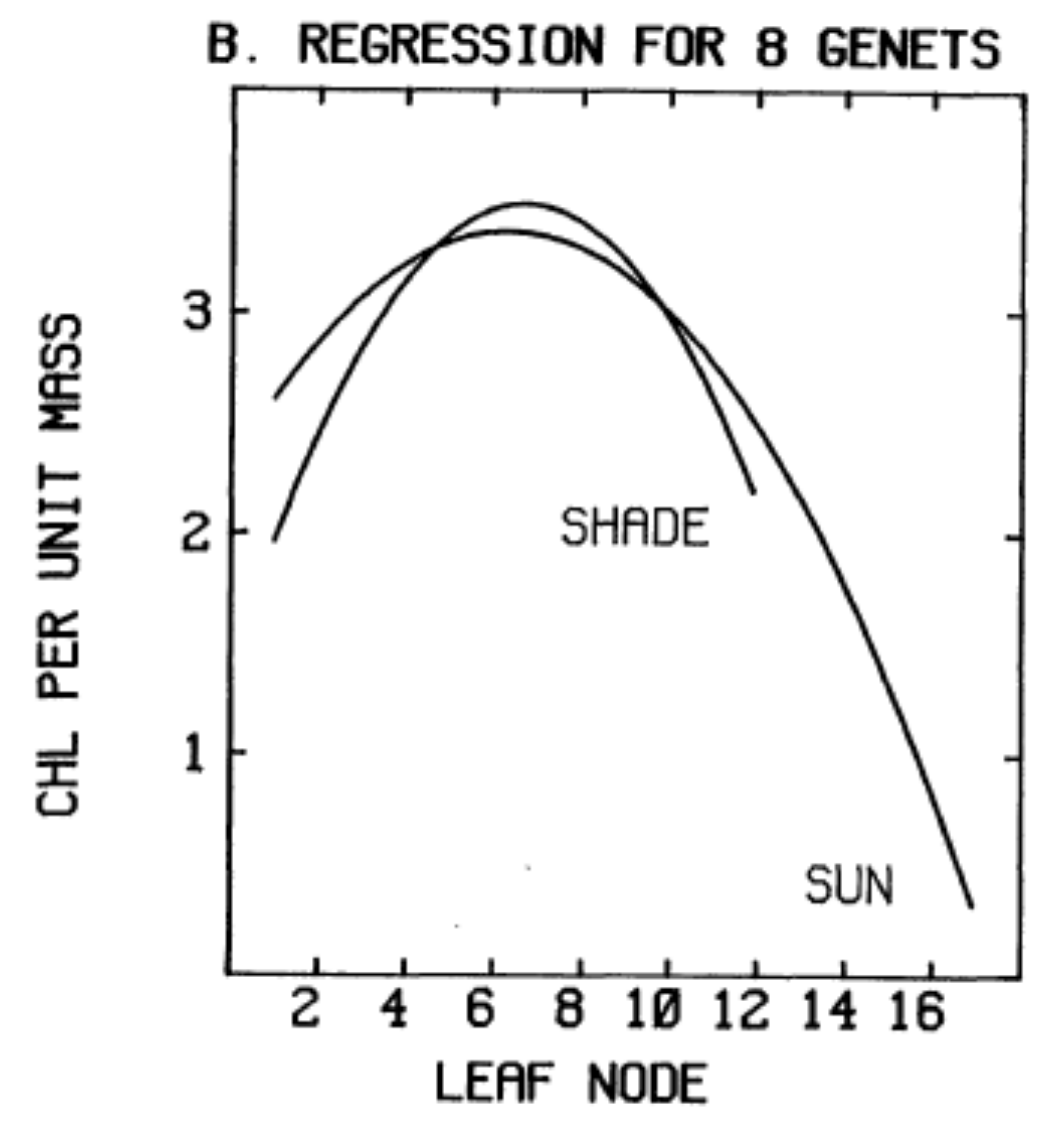
- Variability of leaf chlorophyll content in a population of sassafras. Bulletin of the Torrey Botanical Club 117: 167-172.

n=8
Shade Leaves and Sun Leaves chlorophyll content

Table 2: Mean chlorophyll content mg/g



Tree no.	mg g⁻¹ Shade	Sun	*P*-value
590	8.87	5.04	0.0001
597	5.03	6.79	0.0001
598	4.58	4.82	0.2877
591	10.65	8.73	0.0078
586	7.33	4.18	0.0001
585	8.27	5.59	0.0001
589	4.96	4.18	0.0013
595	6.54	4.29	0.0001
All	7.09	5.59	0.0001



Leaf differences within the organization of a plant

Senecio jacobaea	pyrrolizidine alkaloid concentration (defense mechanisms	Conc. in leaves along the stem decline, but varied among plants	De Boer 1999
Thuja plicata	Leaf longevity	Increase with depth in canopy: however the slope differed among trees	Harlow et al. 2005

Flowers: differences within the organization of a plant

Medrano, Monica, Pablo Guitian, and Javier Guitián. "Patterns of fruit and seed set within inflorescences of *Pancratium maritimum* (Amaryllidaceae): nonuniform pollination, resource limitation, or architectural effects?." *American Journal of Botany* 87.4 (2000): 493-501.

- *Pancratium maritinum*

Flowers open sequentially

General Observations:
Corolla length decline with blooming order of the inflorescence

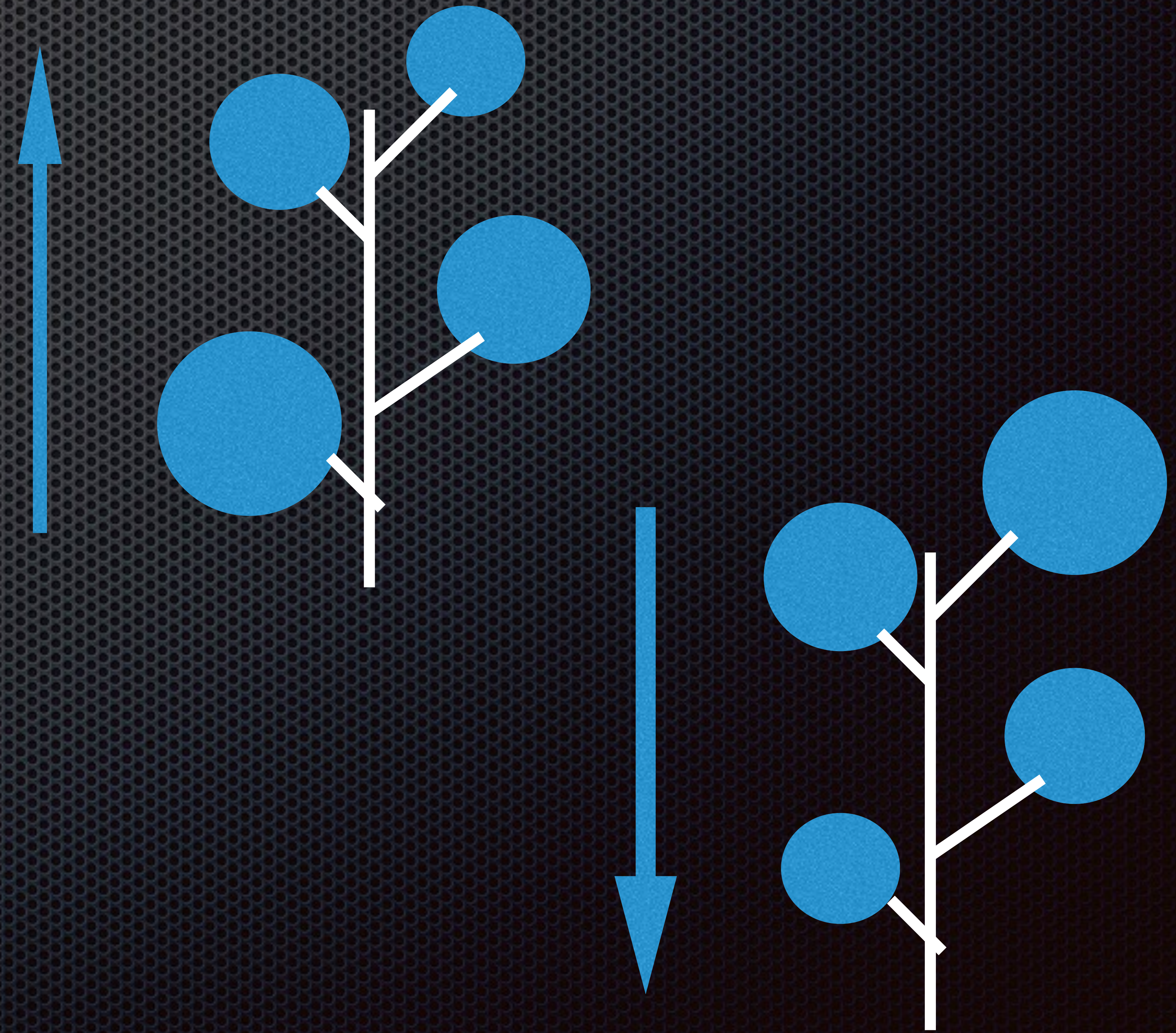
However, the regressions slopes differed significantly among individuals

Herrera calculated the regression of corolla length from Medrano et al's data

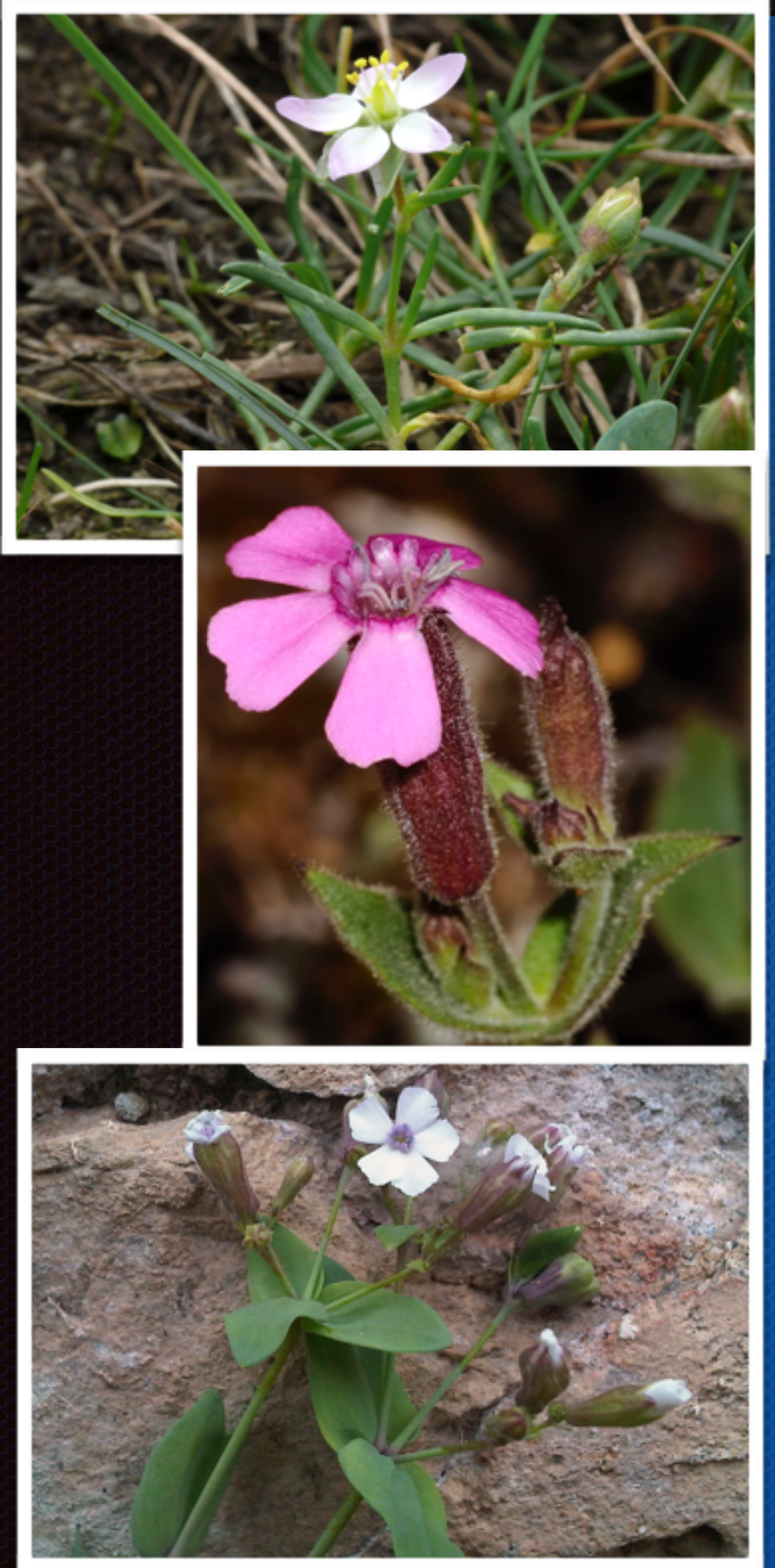
Denotes broad individual range in the magnitude of within plant trend of variation

Slope range from -4.6 mm/position (Sequential decline)

+2.5 mm/position (Sequential increase)



Flowers: differences within the organization of a plant



Spergularia maritima	Number of ovules	Time X maternal family	Mazer and Delasalle 1996
Silene acutifolia	Number of ovules	Decrease from early to later position on inflorescence Rate of decline varied among individuals	Guide 2004
Petrocoptis viscosa	Petal length	Decrease from early to later position on inflorescence Rate of decline varied among	Navarro 1996

Genetic basis for differences in Within-plant trait variability

- Direct support for Wild Plants
- Paxman 1956: *Nicotiana rustica*

A **diallel cross** is a mating scheme used by plant and animal breeders, as well as geneticists, to investigate the genetic underpinnings of quantitative traits
Full diallels require twice as many crosses and entries in an experiments, but allow for testing for maternal and paternal effects.

Wild Tobacco

Paxman 1956: Differentiation and stability in the development of *Nicotiana rustica*, Annals of Botany 20: 331-347.

- Evaluated the within-plant variation in leaf and flower traits.
- Unique is that he considered within individual variation as an ordinary trait
- Complete diallel set of **Selfs**, **F1** and **F2** crosses were grown in 1953 and 1954

Inbred lines = 5
Within plant = 3 Flowers

Evaluated the effect of Pistil and Stamen Length

Table 1: Analysis of **Pistil Length** in the parental families: 1954 data

Item	df	Mean square	p - value
Position (Flower Position)	2	12.72	<0.1%
Between varieties	4	277.27	<<0.1%
Varieties X Position	8	1.86	1%
Plant X varieties	94	0.94	..
Remainder	188	0.71	..

Is subindividual variance heritable?

	Item	df	Mean Square	p-value
a	Lines	4	0.456	<0.1%
b1	Mean Dominance Deviation	1	0.001	
b2	Further Dominance Deviation	4	0.099	
b3	Remainder Dominance Deviation	5	0.055	
c	Line Reciprocal Remainder	4	0.074	
d	Reciprocal Difference Remainder	6	0.103	
Y	Years	1	1.510	<0.1%
C	Characters (subindividual variation)	2	0.001	1-2%
B	Blocks	4	0.054	
	Y x a	4	0.223	2-5%
	Y x the other Main effects	20	0.097	
	C x Main effects	24	0.042	5%
	Y x C x Main effects	23	0.067	
	B x Main effects	94	0.079	

Casella and Ceulemans 2002: Tree Physiology 22: 1277-1288

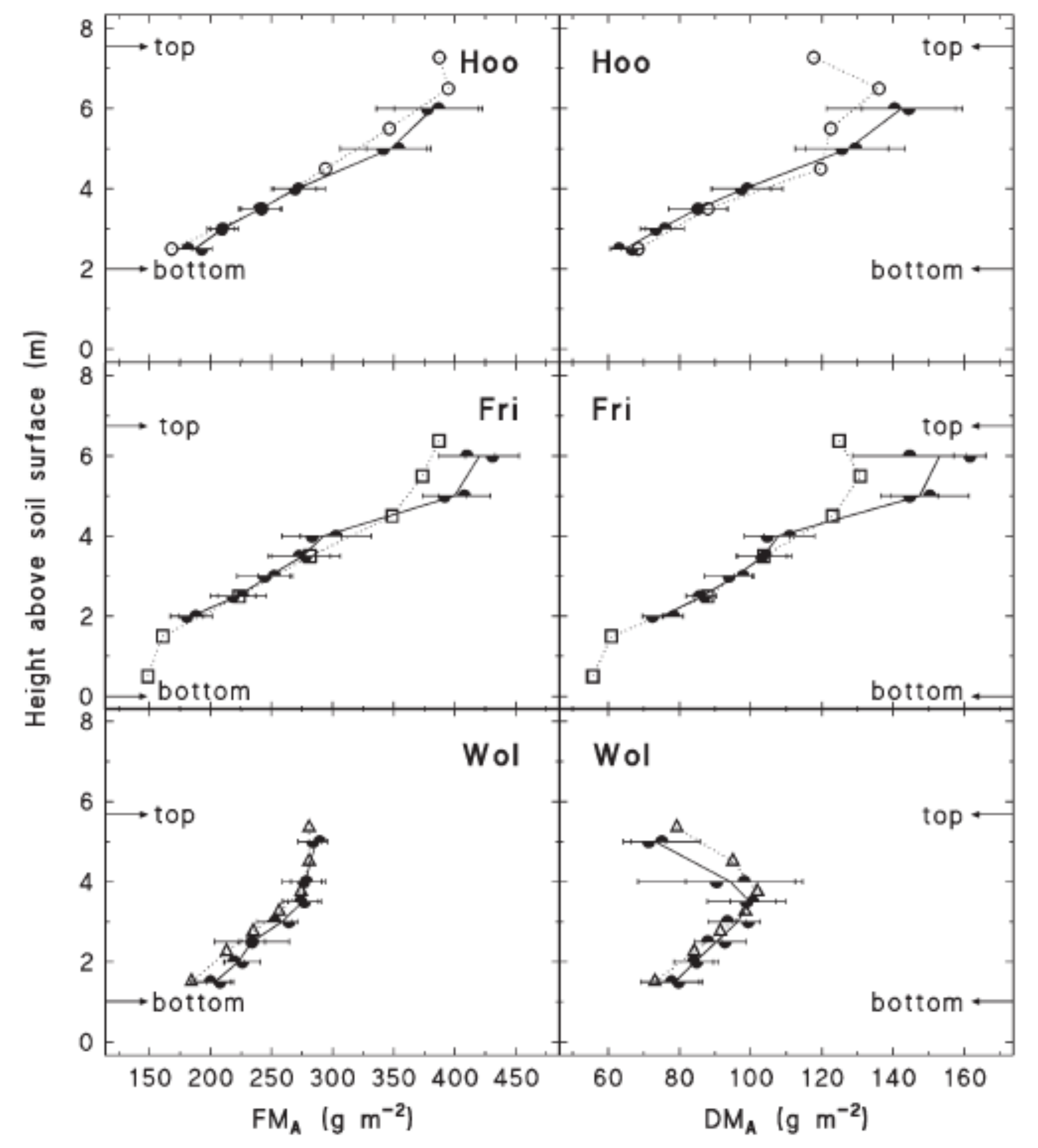


Figure 3. Vertical profiles of leaf fresh mass per unit area (FM$_A$) and leaf dry mass per unit area (DM$_A$) through the canopies of poplar clones Hoogvorst (Hoo), Fritzi Pauley (Fri) and Wolterson (Wol). Values are the means of seven leaf samples taken along the South–North transect (◓), and the East–West transect (◒) inside the canopy, or the results based on scaling-up (Equation 3) (○ = Hoo; □ = Fri; △ = Wol). The horizontal bars depict the standard deviation of the mean. Arrows indicate the bottom and top of the canopy.

Consequences of Sub-individual variation?

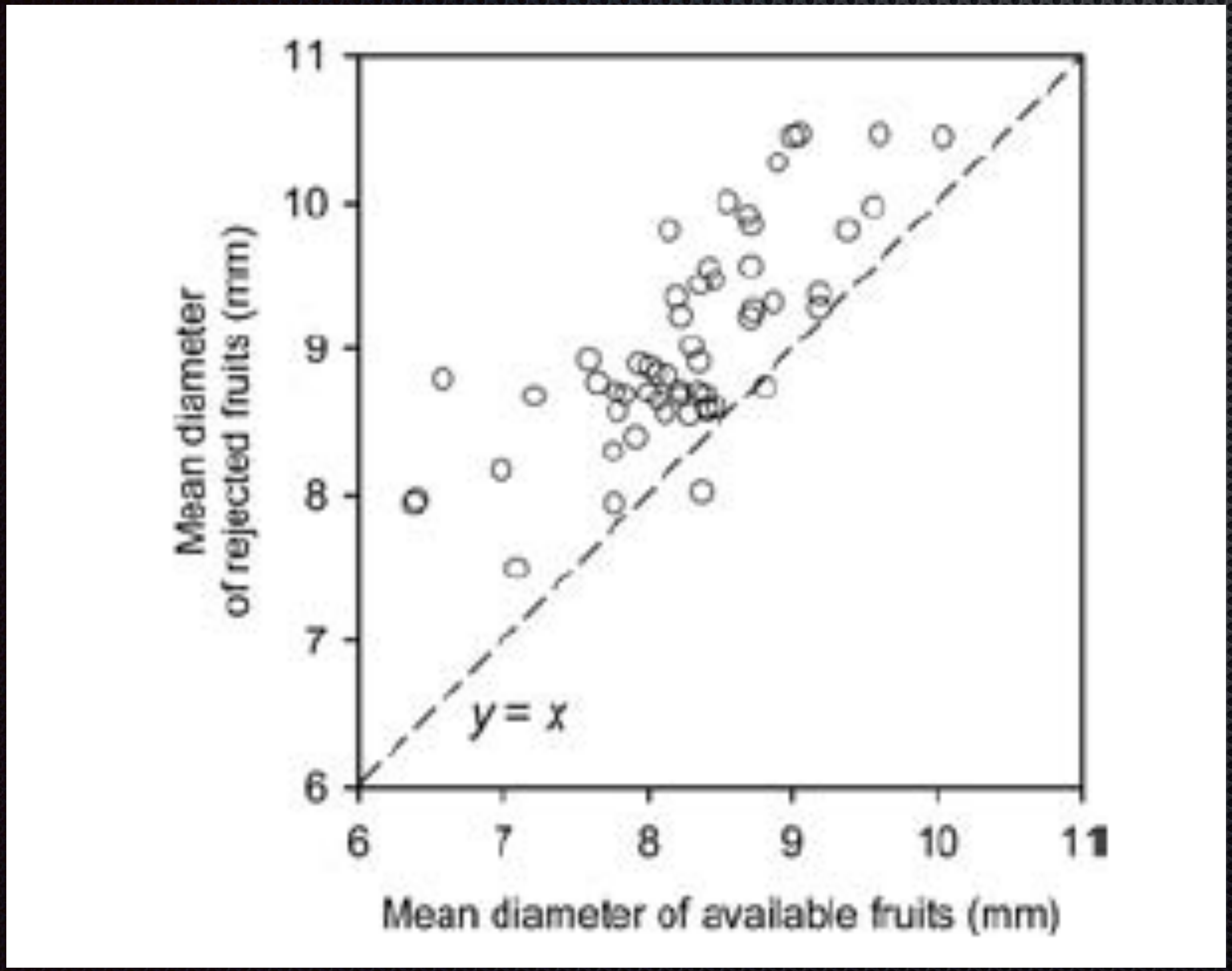
- Sub individual Variation influences plant animal interactions.

Epidendrim secundum

Frugivorous thrushes (*Turdus* app.) fruit size selection while foraging on *Crataegus monogyna*

The size of fruits that are selected are not representative of the distribution


© Janet Pesaturo



- Most nectarivores are variance-averse

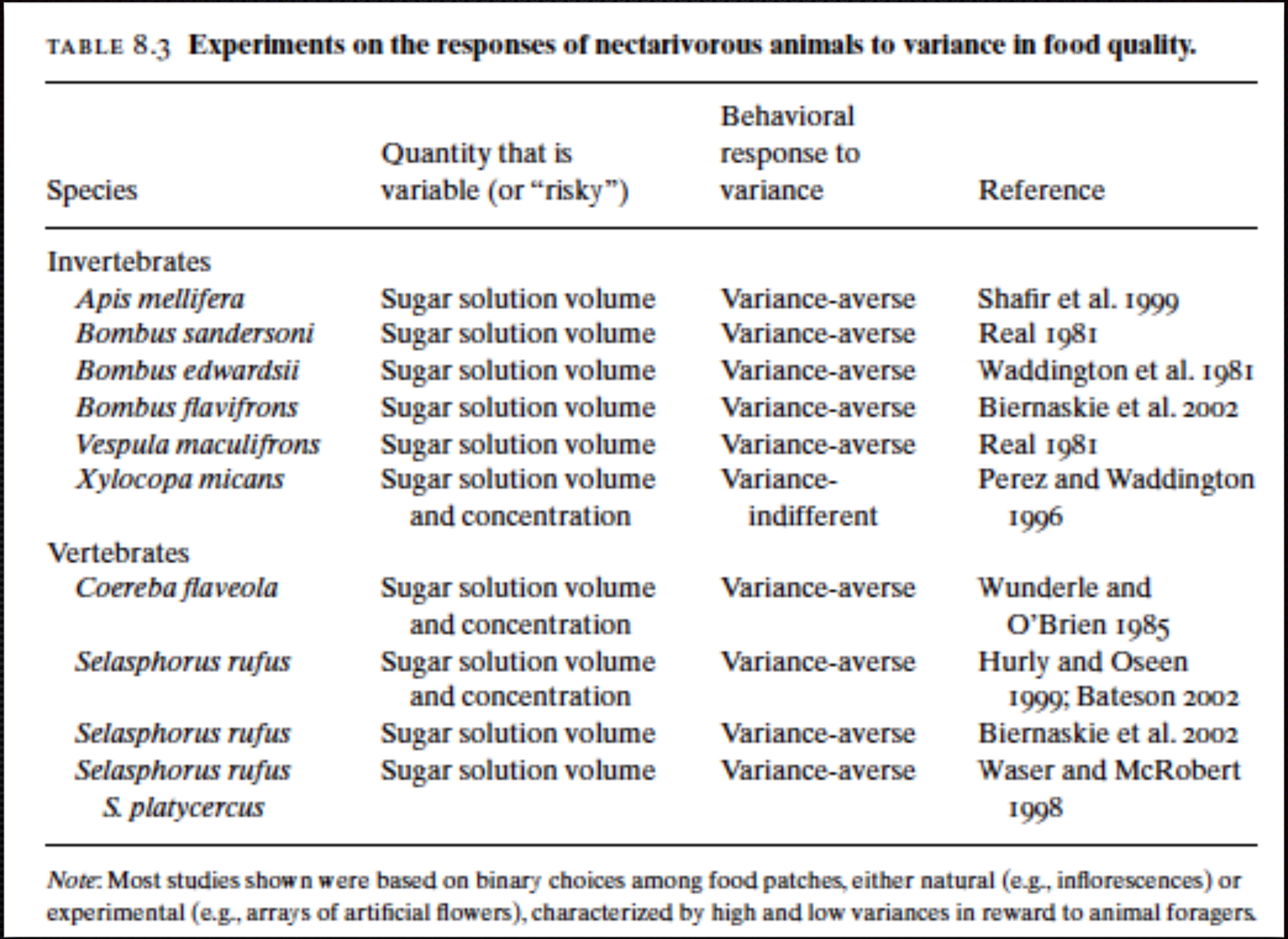


TABLE 8.3 **Experiments on the responses of nectarivorous animals to variance in food quality.**

Species	Quantity that is variable (or "risky")	Behavioral response to variance	Reference
Invertebrates			
Apis mellifera	Sugar solution volume	Variance-averse	Shafir et al. 1999
Bombus sandersoni	Sugar solution volume	Variance-averse	Real 1981
Bombus edwardsii	Sugar solution volume	Variance-averse	Waddington et al. 1981
Bombus flavifrons	Sugar solution volume	Variance-averse	Biernaskie et al. 2002
Vespula maculifrons	Sugar solution volume	Variance-averse	Real 1981
Xylocopa micans	Sugar solution volume and concentration	Variance-indifferent	Perez and Waddington 1996
Vertebrates			
Coereba flaveola	Sugar solution volume and concentration	Variance-averse	Wunderle and O'Brien 1985
Selasphorus rufus	Sugar solution volume and concentration	Variance-averse	Hurly and Oseen 1999; Bateson 2002
Selasphorus rufus	Sugar solution volume	Variance-averse	Biernaskie et al. 2002
Selasphorus rufus *S. platycercus*	Sugar solution volume	Variance-averse	Waser and McRobert 1998

Note: Most studies shown were based on binary choices among food patches, either natural (e.g., inflorescences) or experimental (e.g., arrays of artificial flowers), characterized by high and low variances in reward to animal foragers.

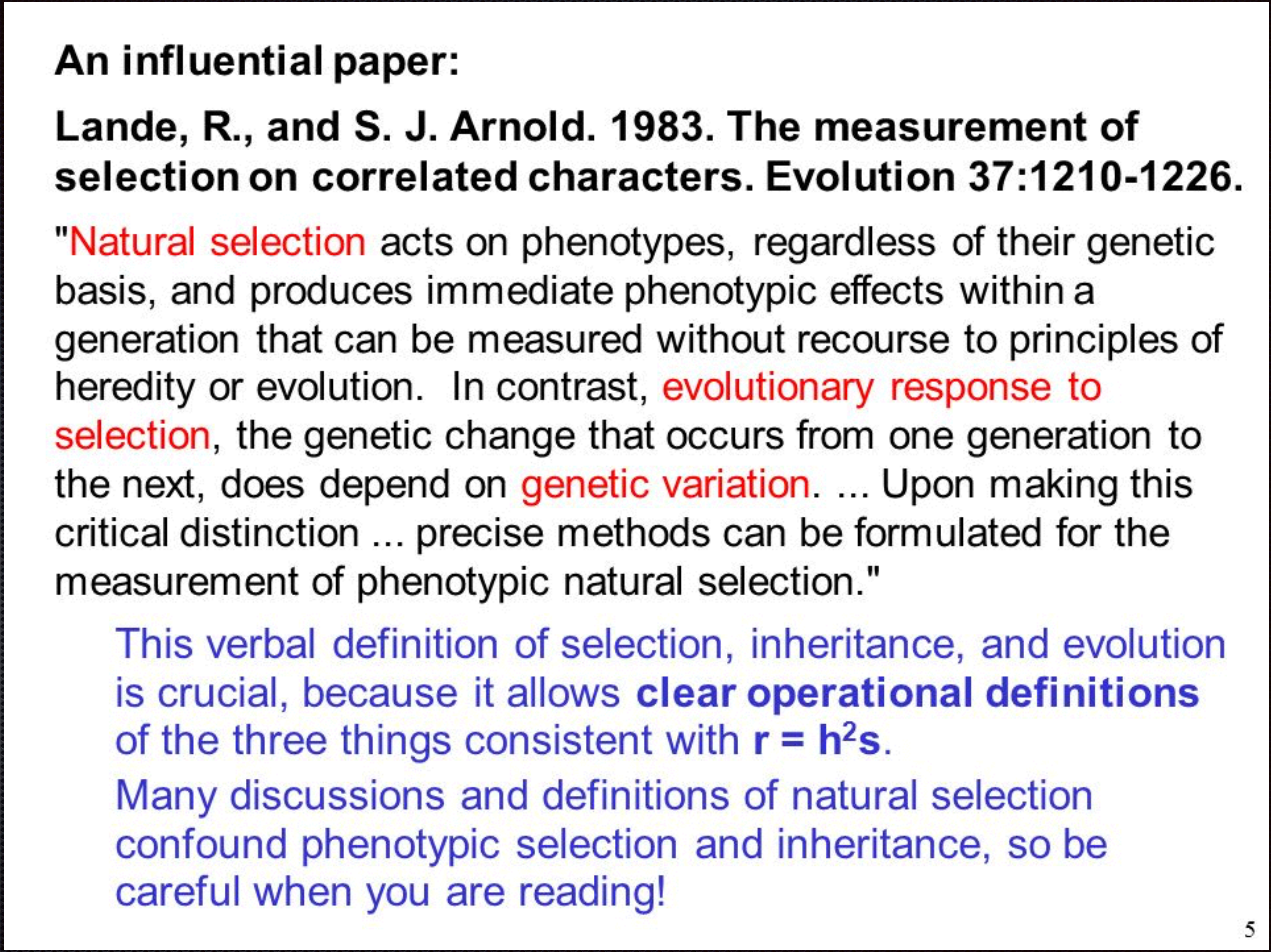
Fitness Consequences of Sub-individual variation?

- A “Variance-Aware” phenotypic Selection model

Lande and Arnold 1983:
Arnold and Wade 1984a, 1984b

Lande, Russell, and Stevan J. Arnold. "The measurement of selection on correlated characters." *Evolution* (1983): 1210-1226.

Cited > 3500



An influential paper:

Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210-1226.

"Natural selection acts on phenotypes, regardless of their genetic basis, and produces immediate phenotypic effects within a generation that can be measured without recourse to principles of heredity or evolution. In contrast, evolutionary response to selection, the genetic change that occurs from one generation to the next, does depend on genetic variation. ... Upon making this critical distinction ... precise methods can be formulated for the measurement of phenotypic natural selection."

> This verbal definition of selection, inheritance, and evolution is crucial, because it allows **clear operational definitions** of the three things consistent with $\mathbf{r = h^2 s}$.
>
> Many discussions and definitions of natural selection confound phenotypic selection and inheritance, so be careful when you are reading!

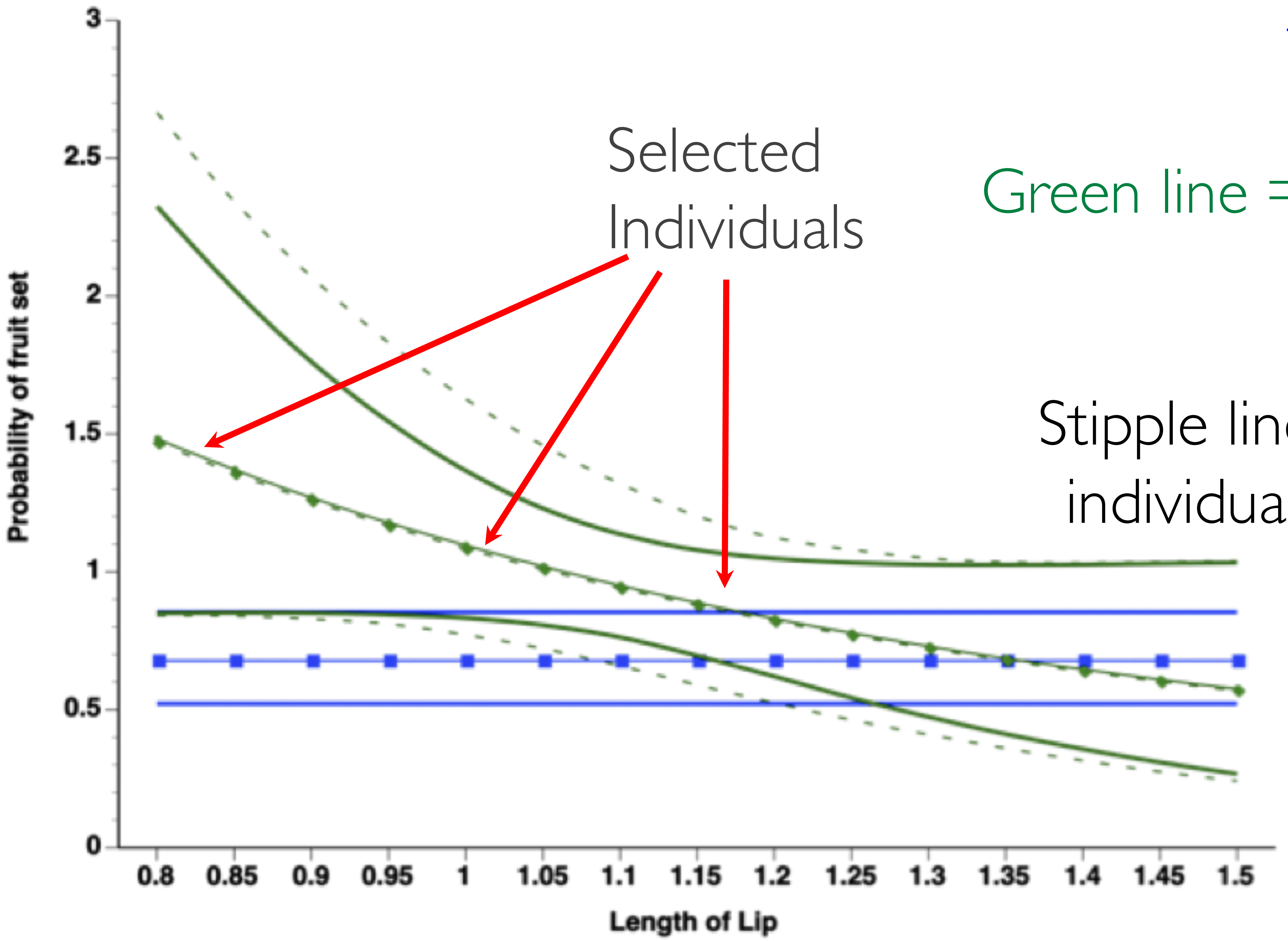
2011
Pearson
Education

The basic Equation for estimating phenotypic selection

$$W=\alpha+\sum b_i X_i$$

W = Fitness measure
b_i = slope= “selection gradient”
X_i = individual values

Tolumnia variegata



Selected Individuals

Blue line = plants in the shade

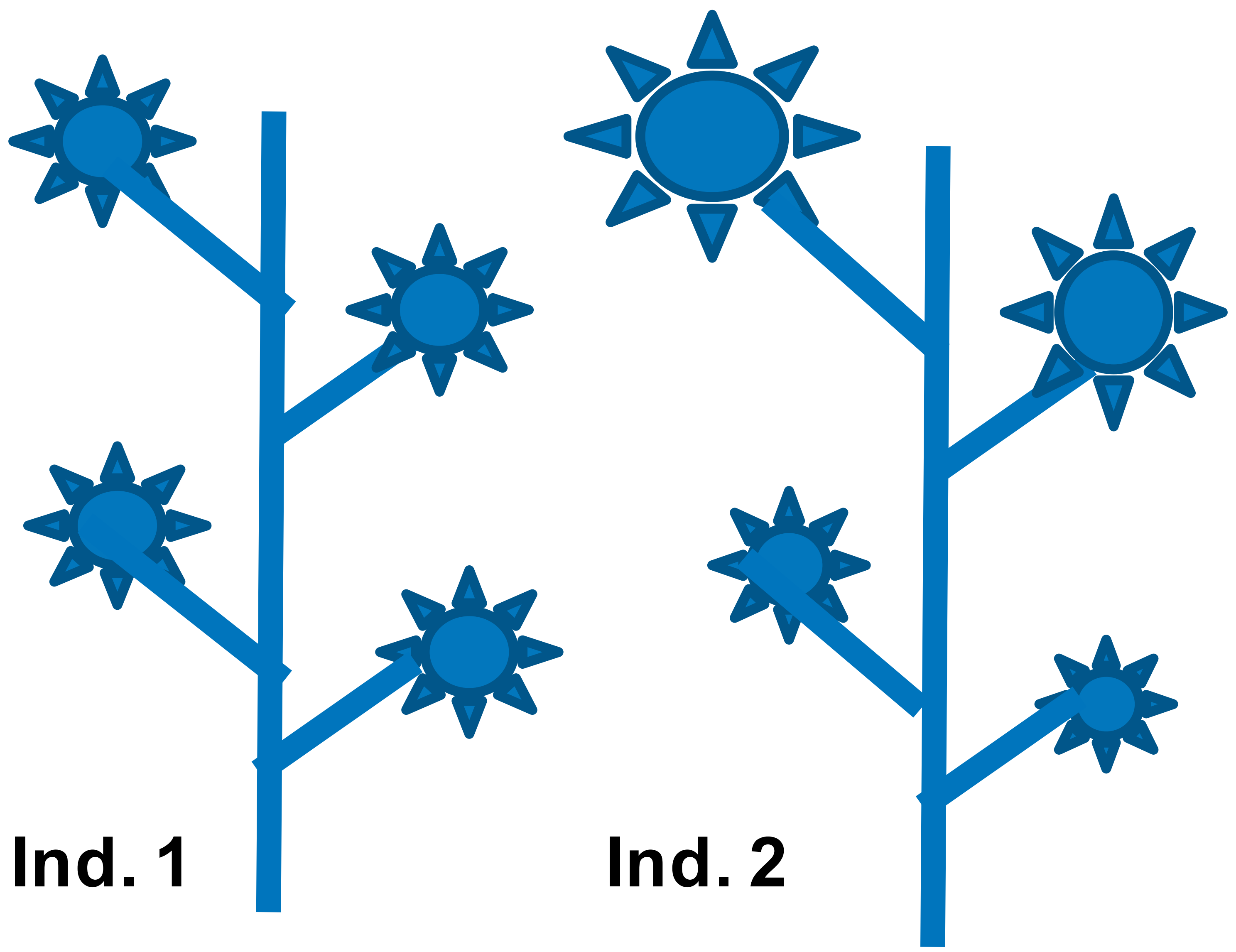
Green line = plants in the sun

Stipple lines include individual variation

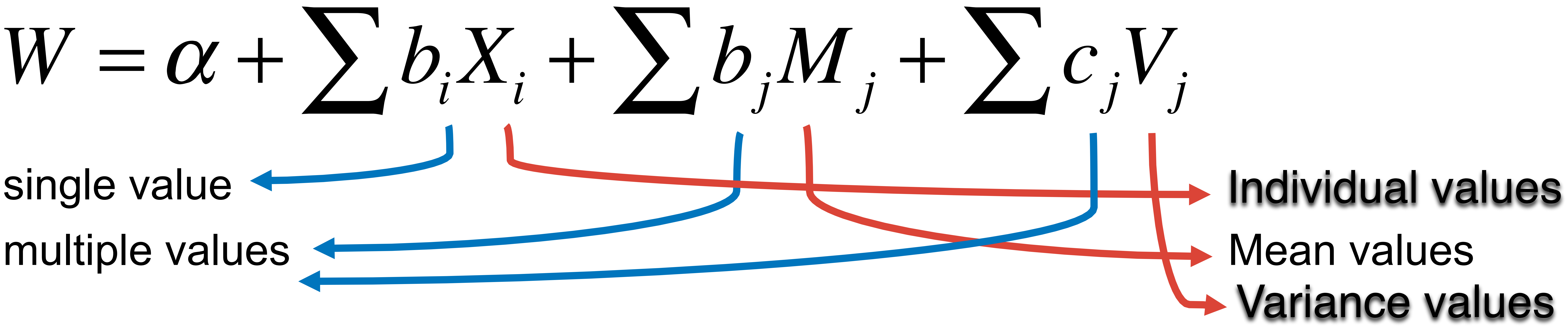
Phenotypic selection landscape of a variable selection surface for the length of the lip (cm) in *Tolumnia variegata* .

Tremblay, Raymond L., James D. Ackerman, and Maria-Eglée Pérez. "Riding across the selection landscape: fitness consequences of annual variation in reproductive characteristics." *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 365.1539 (2010): 491-498.

Carlos Herrera 2009



Within-plant variance (subindividual variation) can be incorporated in the model as potential phenotypic traits subject to selection.



$$W = \alpha + \sum b_i X_i + \sum b_j M_j + \sum c_j V_j$$

i = single value

j = multiple values

Individual values

Mean values

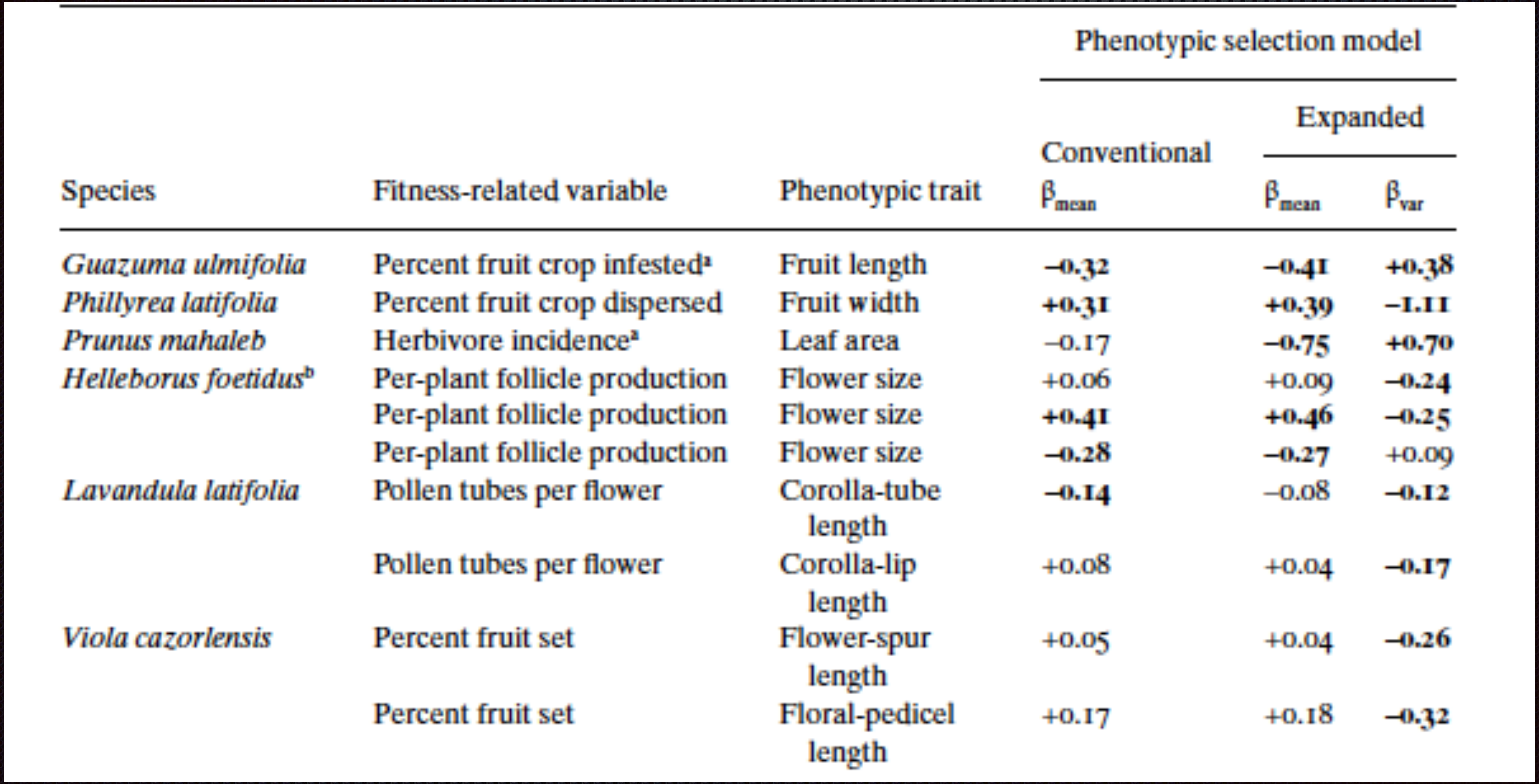
Variance values

Example of conventional and expanded phenotypic selection analysis based on regressing fitness-related measures on traits of fruit and flowers

Expanded version

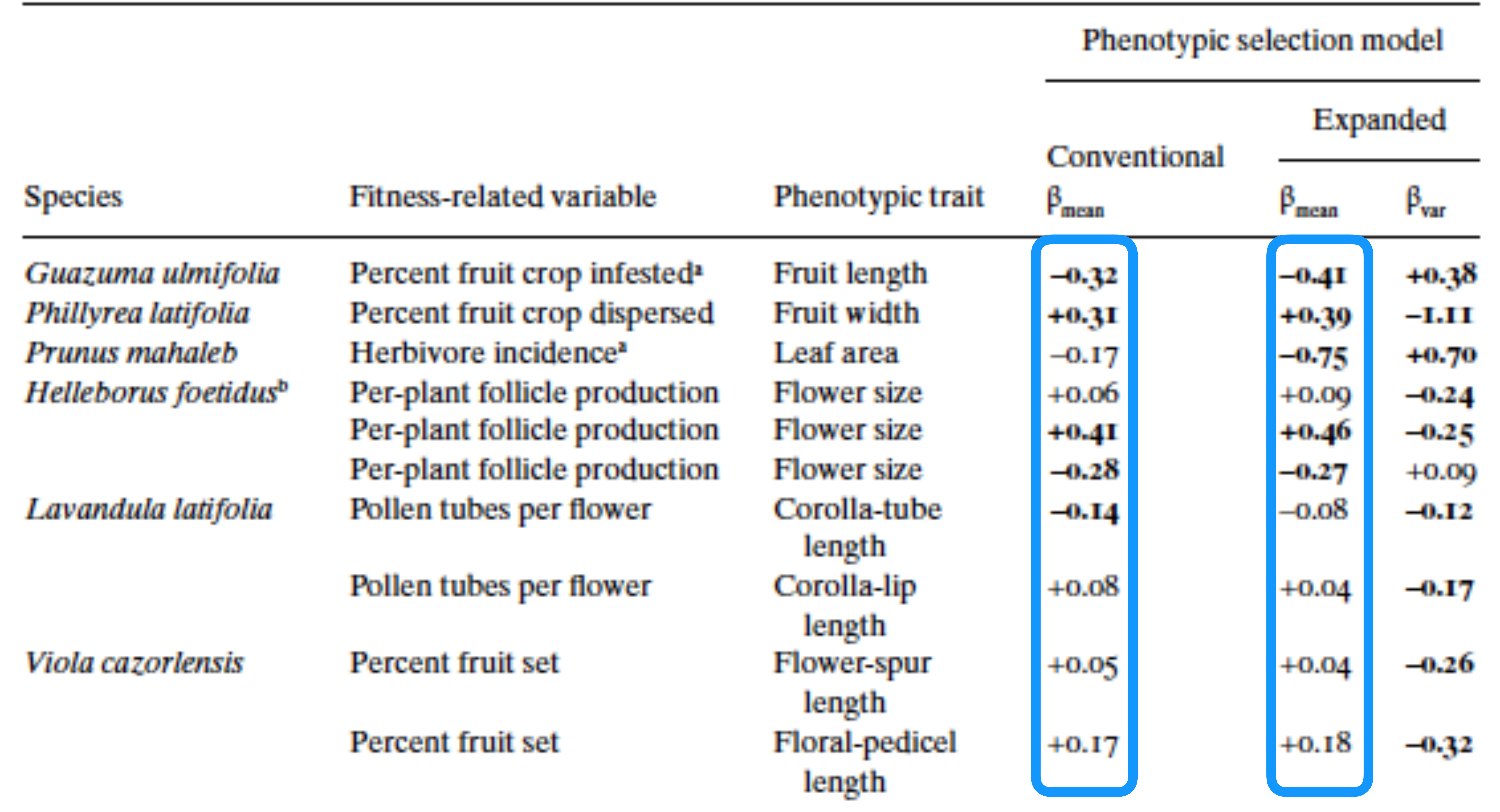
Species	Fitness related variable	Phenotypic trait	Conventional B_{mean}	B_{mean}	B_{var}
Guazuma ulmifolia	% fruit crop infested	Fruit Length	**-0.32**	**-0.41**	**+0.38**
Prunus mahalab	Herbivore incidence	Leaf area	-0.17	**-0.75**	**+0.70**
Lavandula latifolia	Pollen tubes per flower	Corolla-lip length	**-0.14**	-0.08	**-0.12**

Table 10.2: Herrera 2009



			Phenotypic selection model		
			Conventional	Expanded	
Species	Fitness-related variable	Phenotypic trait	β_{mean}	β_{mean}	β_{var}
Guazuma ulmifolia	Percent fruit crop infested[a]	Fruit length	**−0.32**	**−0.41**	**+0.38**
Phillyrea latifolia	Percent fruit crop dispersed	Fruit width	**+0.31**	**+0.39**	**−1.11**
Prunus mahaleb	Herbivore incidence[a]	Leaf area	−0.17	**−0.75**	**+0.70**
Helleborus foetidus[b]	Per-plant follicle production	Flower size	+0.06	+0.09	**−0.24**
	Per-plant follicle production	Flower size	**+0.41**	**+0.46**	**−0.25**
	Per-plant follicle production	Flower size	**−0.28**	**−0.27**	+0.09
Lavandula latifolia	Pollen tubes per flower	Corolla-tube length	**−0.14**	−0.08	**−0.12**
	Pollen tubes per flower	Corolla-lip length	+0.08	+0.04	**−0.17**
Viola cazorlensis	Percent fruit set	Flower-spur length	+0.05	+0.04	**−0.26**
	Percent fruit set	Floral-pedicel length	+0.17	+0.18	**−0.32**

Table 10.2: Herrera 2009



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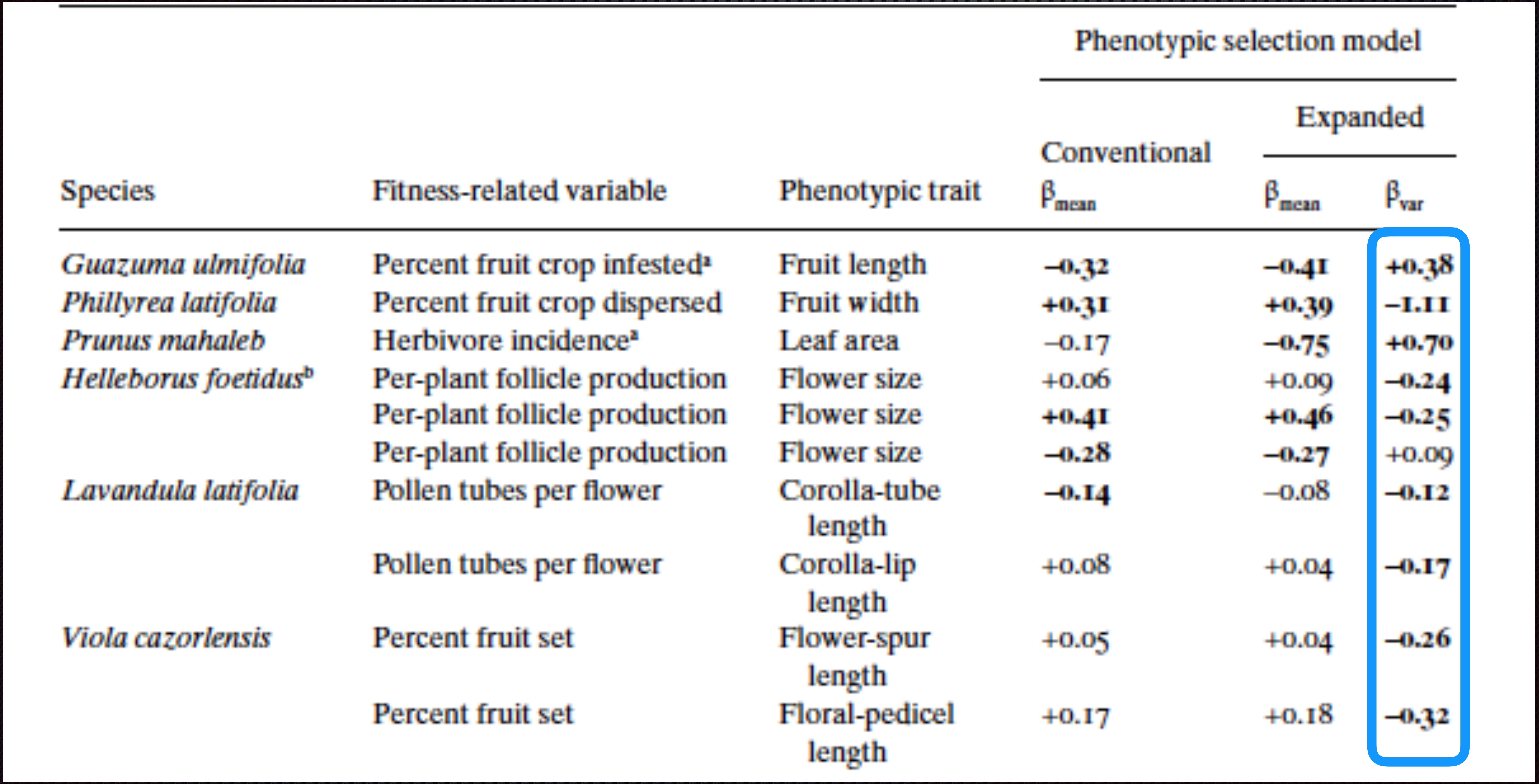

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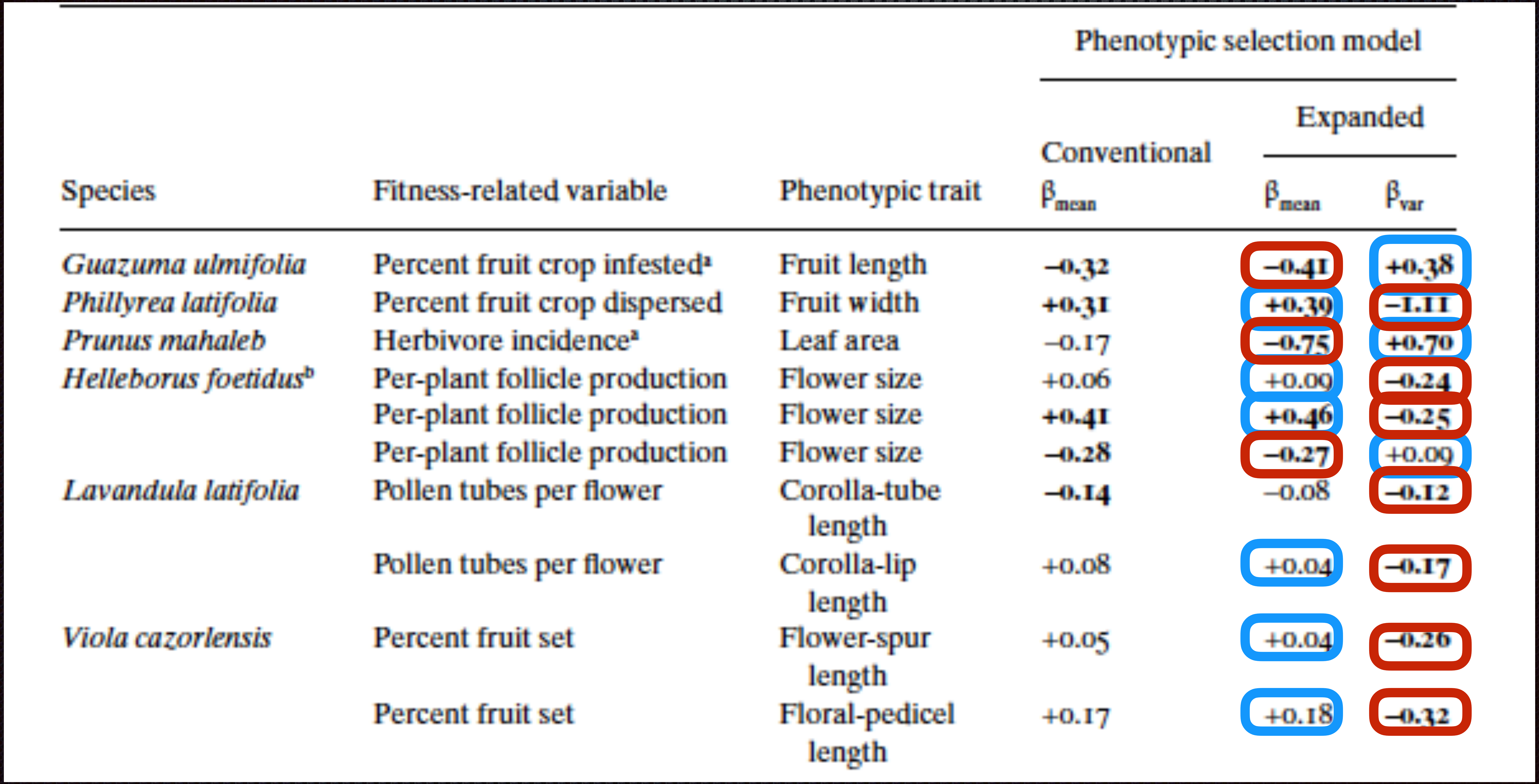

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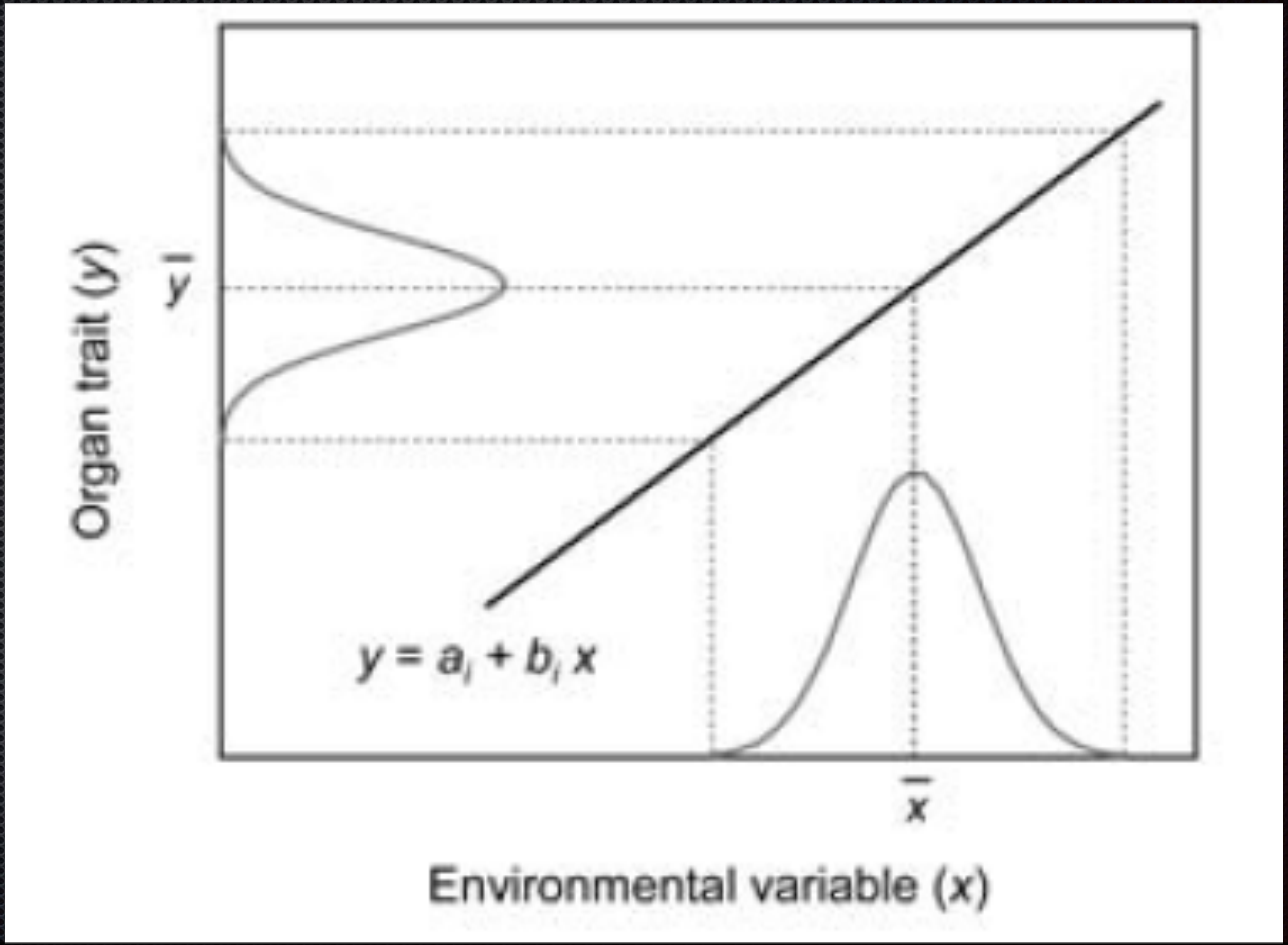
Evolutionary implications of Sub- individual variation?

- Within plant phenotypic frequency distribution of a given organ trait exhibited by an individual plant i.



Distribution of slopes