# Where plants rank

Based on Arumuganathan and Earle, 1991

- The following table is a partial listing. Non-plant values have been added to it
- 1 pg = 965 million base pairs

Species	Common name	Family	DNA Mbp/1C	DNA pg/2C
Escherichia coli			4.6	0.04
Genlinsea tuberosa	Corkscrew plant	Lentibulariaceae	61	0.13
Drosophila melanogaster	Fruit fly		130	0.24
Arabidopsis thaliana	Mouse-ear cress	Crucifereae	145	0.30
Oryza sativa	Rice	Gramineae	415	0.86
Phaseolus vulgaris	Bean	Leguminoseae	637	1.32
Musca domestica	House fly			1.78
Glycine max	Soybean	Leguminoseae	1115	2.31
Zea mays	Maize	Gramineae	2292	4.75
Homo sapiens	Human			6.00
Pisum sativum	Реа	Leguminoseae	3947	8.18
Hordeum vulgare	Barley	Gramineae	4873	10.10
Gryllus domestica	Crickett			12.00
Bufo bufo	Toad			12.00
Allium cepa	Onion	Amaryllidaceae	15,290	31.69
Triticum aestivum	Wheat	Gramineae	15,966	33.09
Amphiuma means	Congo eel			170.00
Fritillaria platyptera+++		Liliaceae	84,150	174.40
Paris japonica	Japanese canopy plant	Melanthiaceae	149,000	304.46

+++ True diploid (2n = 2x = 24) with largest genome

# **C-value paradox**

#### Thomas, 1971

There is no relationship between complexity of an organism and the amount of DNA

- Known as the C-value paradox
- Implies that much DNA must be non-coding for genes

# Angiosperm DNA C-values Database Pellicer & Leitch, 2020

- Plant DNA C values can be found at https://cvalues.science.kew.org/
- 1 pg = 978 million base pairs (value from Delezal et al, 2003)



# **Range in angiosperm DNA content**

Heslop-Harrison and Schwarzacher, 2011



Minimum genome size:

- Average genome has 30,000 genes
- Average exon size per gene is 1346 bp
- Thus, gene space = 40 Mb
- Telomeres, centromeres, rDNA, introns, promoters add another 20 MB

Smallest genome size for a plant should be ~60 Mb

# Smallest genome size

Heslop-Harrison and Schwarzacher, 2011 Fleischmann et al, 2014

> Genlinsea aurea DNA Mbp/1C = 63 DNA pg/2C = 0.13



Genlinsea tuberosa DNA Mbp/1C = 61 DNA pg/2C = 0.126



http://cpphotofinder.com/genlisea-aurea-516.html

# Largest plant genomes

Pellicer et al., 2010



Paris japonica, 2n = 40, Wikipedia



#### VII-C – Changes in DNA content PBGG 8900 Spring 2025 | page 4 Fernández et al, 2024 (https://doi.org/10.1016/j.isci.2024.109889)

There is a small fern that has even more DNA than *Paris*.



# **Changes in DNA amount & chromosome size**

#### Review by Walbot & Cullis, 1985

Between changes in chromosome size and number, there are large differences in DNA content within



plants.

Family	Species	n	Chromosome length (μm)
Ranunculaceae	Isopyrum fumarioides	7	1.3
	Anemone hepatica	7	7.0
Oxalidaceae	Oxalis cuneata	6	1.5
	Oxalis dispar	6	15.1
Leguminoseae	Lotus tenuis	6	1.8
	Vicia faba	6	14.8
Droseraceae	Drosera rotundifolia	10	0.8
	Drosophyllum lusitanicum	6	14.0
Compositae	Agroseris heterophylla	9	2.4
	Chaetadelpha wheeleri	9	6.4
Liliaceae	Tofieldia nuda	15	1.3
	Lilium pardalinum	12	20.0
Gramineae	Chloris barbata	10	1.5
	Secale cereale	7	7.2

#### VII-C - Changes in DNA content PBGG 8900 Spring 2025 | page 5 Genome size variation in Poales vs WGDs Winterfeld et al, 2025

- All Poales share  $\sigma \& \tau$  WGDs. Only grasses underwent the  $\rho$  WGD
- Yet, all Poaceae do not have 2x the DNA content of Poales → genome reduction in some lineages



Slide concept by Catherine Feuillet



# The increase/decrease model

#### Vitte and Panaud, 2005

Increase : - Retrotransposition



#### Piegu et al, 2006 (graphics by O Panaud)

• Doubling of rice EE genome size due to retrotransposition



#### Hawkins et al., 2009

3x genome size differences in diploid cottons due to Gorge3 retrotransposons

- Expansion/contraction rates are lineage-specific, but
- Loss can be fast enough to balance expansion in some lineages



# Number of genes to make an angiosperm?

#### Argout et al, 2011; Shulaev et al, 2011

Estimated minimal gene number by comparison between eudicots and a monocot



Within a given group of organisms (e.g., the angiosperms)

- The gene number can be expected to remain fairly constant.
- There has been an assumption that it takes as many genes to make a corkscrew plant (0.13 pg DNA / 2C) as it does to make a blood lily (222 pg DNA /2C).

# Number of genes per monoploid genome

#### Goldberg, 1986

Working with tobacco, determined that it took about 70,000 genes to make a plant, by counting the number of RNA types present

- This number should probably be halved, as tobacco is an allotetraploid
- Thus it takes 35,000 genes to make a plant

#### Edwards et al, 2017

The tobacco reference genome obtained 69,500 gene models

#### Gibson and Sommerville, 1993

Arabidopsis = 145,000 kb of DNA For dicots

- the average mRNA = 1.34 kb long
- the average intron = 215 bp long
- The average arabidopsis gene has 3.13 introns + untranslated 161 bp at the 5' end and 232 at the 3' end
  - $\therefore$ , primary transcript = 1.34 + (3.13 × 0.215) + 0.161 + 0.232 = 2.4 kb
- Assume average gene needs 0.4 kb 5' and 0.2 kb 3' from regulatory sequences, then each gene = 3 kb in length
  - Then, 145,000 ÷ 3 = 43,500 genes
- If assume there is 1 kb between genes, then gene number = 33,000

#### **Arabidopsis sequence**

#### Wang et al, 2022

Initial estimate is that arabidopsis has 25,725 genes that code for proteins

- Additional genes code for RNAs of different sorts
- Latest estimate is 27,583 nuclear protein-coding genes from Col-0 (TAIR10.1 annotation)

# Sequenced angiosperm genomes

- CoGepedia https://genomevolution.org/wiki/index.php/Sequenced\_plant\_genomes
- Wikipedia <u>https://en.wikipedia.org/wiki/List of sequenced plant genomes</u>
- •





- Rosids
  - 18,397 marula tree 73,013 for Poplar
- o Asterids
  - 14,474 for milkweed 52,232 for Sunflower
- o Grasses
  - 25,225 for moso bamboo 107,891 for wheat
- o Other monocots
  - 19,623 for duckweed 52,342 for *Daemonorops jenkinsiana*

# **Besides protein-coding genes**

#### Cacao - Argout et al, 2011

- 28,798 protein-coding genes
- 6 rRNA genes (many missing due to sequencing method!)
- 473 tRNA genes
- 83 miRNA genes
- 67,575 transposable elements (25.7% of assembly)

#### Strawberry - Shulaev et al, 2011

- 34,809 protein-coding genes
- TE's = 22% of genome
- 569 transfer RNAs (tRNAs)
- 177 ribosomal RNA (rRNA)
- 111 spliceosomal RNAs
- 168 small nucleolar RNAs
- 76 micro RNAs
- 24 other RNAs





#### Bladderwort – Ibarra-Laclette et al, 2013

- 28,500 protein-coding genes but genome is only 77 Mbp
   Shorter promoters and introns; fewer introns
- Only 3% of DNA is repetitive
- Only 579 transposable elements
  - o 375 are retroelements
  - 95 intact (and supposedly functional)
- All miRNA genes are there



# **Copy Number Variation (CNV)**

CNV - when some genotypes have more copies of a given gene per genome than others PAV - when some genotypes lack a copy of a given gene

#### CNV

May represent regional adaptations/stress resistance/functional adaptations

- Creation of duplications
- Loss of duplicated genes from fractionation

Eg, Cyst nematode resistance in soybean **Cook et al, 2012** 





Fiber FISH illustration of CNV for cyst nematode resistance in soybean

# **Presence Absence Variation (PAV)**

# Prem2-b Prem2-b

*Intraspecific violation of genetic colinearity and its implications in maize* Sequenced a 120-kb region around the bz locus in maize.

• Two genotypes: McC is a maize line used in genetic analysis, and B73 is an unrelated standard inbred.

McC has 10 genes in the region, B73 only has 6.

Fu & Dooner, 2002

• Genes with plus-minus variation in the *bz* genomic region were members of multigene families (other copies present somewhere else in the genome of B7).

Hypothesize that lines lacking different genes would complement one another and show hybrid vigor

- May be the basis of heterosis- crossing plants that have complementary missing genes.
- Inbreeding depression would be due to missing genes

# The pangenome concept

#### Review by Della Coletta et al, 2021

Definitions & diagram from http://www.10wheatgenomes.com/

#### Pan genome

• All genes and genetic variation within a species

#### **Core genome**

Portion of the pan genome common to all individuals in the species •

#### **Dispensable genome**

Portion of the pan genome that is only in a subset or unique to individuals

#### PAV in Brassica oleracea

# Agnieska et al, 2016



- 81.3% of genes always present (49,895)  $\rightarrow$  Core genome
- 18.7% are in variable numbers (11,484) → Dispensable, variable,
- 02.2% are present in only 1 line (1,322)
- or shell genome

Pan Genome



# PAV in *Glycine*

Li et al, 2010 (S Jackson lab)





Gene families unique to each genotype

As more wild soybean genomes are compared, the total number of identified genes increases (Pan)

• However, with each additional line that is compared the total number of shared genes decreases (Core)

#### **PAV in grapevine**

#### Da Silva et al, 2013

SP

SLC

"Aromas and flavors of black berry custard tart, chocolate gelato, and praline with a fruity body and a long cranberry chutney and floral honey finish"

Popular wine grapes contain hundreds of genes not found in the reference genome

# PAV in tomato Gao et al, 2013

SLL





#### 725 varieties

- 4,873 genes present in just some genotypes
- Mainly genes for stress resistance and adaptability



#### **PAV in maize**

#### Springer et al, 2018

- B73 6,440 unique genes + 1394 unique tandems
- W22 8,372 unique genes + 1261 unique tandems + 177,000 transposons



https://www.pacb.com/blog/sequencing101pangenome

# Pan genome hypothesis for

# heterosis

#### Tao et al, 2019

As originally proposed by Dooner, adding missing genes leads to heterosis



#### Hemizygosity

#### Peng et al, 2018

• Hemizyous loci are more common in vegetatively propagated crops, and least common in selfers, with outcrossers being intermediate



Trait accumulation in conventional plant breeding

#### IRRI 1980 Annual Report

- Plant breeders stack desirable traits into elite genotypes
- These traits are found by screening genotypes, then crossing them in

	IR8	IR42
Blast	MR	R
Bacterial Blight	S	MR
Grassy Stunt	S	R
Tungro	S	R
Ragged Stunt	S	R
Green Leafhopper	R	MR
Brown Planthopper	S	R
Stem Borer	MS	MR
1966/77	Susceptible; I	Resistant



#### Long et al, 2024

- Looked at dispensable genomes in wild (n=5) and in cultivar (n=9) grapes
   Present in at least 2 accessions, but not in all of them
- Genes from the dispensable genome predominate in cultivars, showing how breeders have selected for rare variants and stacked them in elite genotypes



# **Reevaluating the backcross**



#### **Emerging view**

Besides allele replacement, backcrossing can introduce a PAV gene
Can also eliminate genes that were there



## Super pan genome

#### Khan et al, 2020

- The pan genome is at the species level.
- The super pan genome is at the genus level.



Trends in Plant Science

# Using a super pangenome

Li et al, 2023 (https://www.nature.com/articles/s41588-023-01340-y)

- Cytochrome P450 gene, Sgal12g015720
  - $\circ$  244-bp deletion in 1st exon of domesticated tomato
  - $\circ$   $\,$  OE of WT in tomato increases branch number and fruit set

а		000 pp	255	bp A98 bp	,000 br
Sly	/12	30 <sup>,781,0</sup>	60,782	a0,182	60,784
S. lycopersicoides S. habrochaites S. pennellii S. chilense S. peruvianum S. corneliomulleri S. chmielewskii S. pimpinellifolium S. galapagense S. lycopersicum A S. lycopersicum B S. lycopersicum B					
		> > > > > >	· · · · · ·	· · · · · · · ·	3 3

Sgal12g015720



# **Origins of PAV**

#### **Helitrons**

#### Lai et al., 2005

In maize, arises due to the movement of genes or gene fragments by Helitrons, a recently discovered class of transposons.

Helitrons were found computationally in *Arabidopsis*, rice, and *C. elegans* 



Had been undetected, because they lack structural features such as terminal inverted repeats or target site duplications

The definition of their ends is facilitated by the identification of their vacant sites in Helitronminus lines

HelA is 5.9-kb long and contains sequences from three of the four genes found only in the McC bz genomic region, found in 5S location in B73.

Also found in morning glory. Serve same function as packmule elements in rice and Express elements in soybean

#### VII-C - Changes in DNA content PBGG 8900 Spring 2025 | page 19 Fractionation/differential gene loss Modified from Vision, 2005 Town et al, 2006

Eg, about 35% of genes have been lost after genome duplication in Brassica

- Some genes also get fragmented and dispersed throughout the genome
- Leads to over-counts of gene number from genomic sequences



#### Eichten et al, 2011; Schnable et al, 2011

In addition, differential gene loss of genes from the genomes of the parents that give rise to an alloploid species lead to PAV



Although the Vision model is being used here to show PAV at the species level, Vision meant for it to explain it between species.

• I.e., this model is scalable

#### Gene loss through intra-strand recombination

#### Woodhouse et al., 2010

Genes most likely to be lost are flanked by direct repeats in their ancestral genome

• Permits loss due to intra-strand recombination



# **Genome downsizing**

#### Leitch & Bennett, 2004

Lower C-values than expected from sum of parental subgenomes

• Thought to result from DNA losses as detailed above and reflects trend of genome downsizing

"DNA C-values and basic genome sizes in 'all angiosperms' with known C-values and even ploidies between 2x and 12x. A, Mean 1C DNA values observed (•) compared with expectation () at six different ploidies assuming C-value and ploidy are directly propo proportional. B, Minimum, maximum and mean (•) C-values at each ploidy."



#### **Creation of new genes**

#### Fan et al., 2008

Since lots of recombination and transposon insertion goes on in subtelomere regions, that is where a lot of new genes are formed.

- Looked at 12 genes in the subtelomere region for rice chromosome 3
  - These were paralogues of older genes
- 9 were functional
  - o 5 were chimeric- ie, made of segments of multiple other genes
  - 2 were defense/stress-related

# Genome sequence summary & caveats

Initial concept that genes within a species were constant is wrong

- Talk about "reference" genome for a given crop, rather than "the" genome
- Almost all genomic sequences are incomplete
- Still do not know how to recognize all genes in a sequence
- Exon/intron prediction is not exact
- Promoters still guessed at
- Gene annotation is very limited. Most are of unknown function.
- Assumption that all plants have the same genes is wrong
  - o Different lineages amplify genes for specific purposes
  - o E.g., poplar has more genes associated with wood formation

# Gene space in the plant genome

#### Barakat, Matassi, & Bernardi, 1998

The area of chromosome containing a high density of genes is known as the gene space

 Tomato: most genes in just 5% of the genome [Wang et al., 2005. TAG 112-72-84].

The original concept was that gene-space would be distributed in clusters evenly spread along the length of a chromosome.

With sequence in place, the pattern is clear:

- Gene density increases near telomeres
- Gene density correlated with crossover frequency







#### The Potato Genome Sequencing Consortium, 2011

- a Chromosome karyotype | centromere
- b Gene density (genes per Mb) 0
- c Repeats coverage (%) 0
- **d** Transcription state
- e GC content 30 40 50 (GC%, bin = 1 Mb)
- f Subtelomeric repeats distribution



# **Adaptive Value of DNA Content** Environmental effects on genome size

Kalendar et al, 2000

Looked at number of BARE1 copies in barley from Evolution Canyon, Mt. Carmel, Israel

- Plants from the drier south slope had greater numbers
- Plants from the higher altitudes had higher numbers



# **Cell size vs DNA content**

There is a relationship between DNA content and size.

- Remember from prior lectures that cell volume is a function of DNA content
- The same relationship is also evident in these tobacco cells



Epidermal cells of 2x, 4x and 8x Nicotiana. Greenleaf, 1938

#### Knight & Beaulieu, 2008; Pellicer et al, 2010

Applies between species as well:

• Right, stomate of Paris japonica, the largest angiosperm genome known to date



Paris japonica 2C = 304.46

White scale bar in (A) = 20 µm. (A) *Citrus* aurantifolia, (B) *Rosa acicularis*, (C) *Origanum vulgare*, (D) *Quercus robur*, (E) *Fraxinus excelsior*, (F) *Ligustrum vulgare*, (G) *Platanus orientalis*, (H) *Cypripedium irapeanum*, (I) *Capsicum annuum*, (J) *Zingiber officinale*, (K) *Sambucus racemosa*, (L) *Tradescantia paludosa*, (M) *Cypripedium formosanum*, (N) *Paeonia clusii*, (O) *Tradescantia virginiana*.

#### **Constraints on cell size**

#### Ohri, 2008

- Herbaceous angiosperms tend to have more DNA than woody angiosperms
- Woody gymnosperms, however, have variable amounts of DNA
  - This constraint thought to be due to the limit on the size of the nucleus in the cambial cells in woody plants that give rise to xylem and phloem
  - o Angiosperm vessel elements vs gympnosperm tracheids conduct water differently
  - o If the vessel element diameter gets too large, it becomes tough to conduct water.



# VII-C - Changes in DNA content PBGG 8900 Spring 2025 page 25 DNA content vs fitness

#### Vinogradov 2003

Diploid plants with more DNA are overly represented on the endangered species list:



Not due to polyploidy per se or chromosome number, but to life cycle

• Suggests DNA per se can be deleterious

What role does DNA content play in adaptiveness?

#### The nucleotype

#### Bennett, 1972

Concept of a nucleotype: The physical amount of DNA present affects the phenotype independently of the genotype

- In general, monocots have more DNA than eudicots.
- Within each of these, primitive groups have more DNA than derived groups
  - Liliales > orchidiales
  - Ranales > asterales (formerly composites)

As plants evolve from perennial to annual, the amount of DNA decreases

#### DNA content vs cell cycle time

#### Van't Hopf and Sparrow, 1963; Bennett, 1971

As plants evolve from perennial to annual, the amount of DNA decreases

- As the amount of DNA decreases, the cell cycle speeds up, as there is less DNA to replicate
- There is a linear relationship between DNA content and cell cycle time
- DNA content also influences the duration of meiosis
  - o With a linear relationship between DNA content and the duration of meiosis



# **DNA content vs growth**

#### **CORN VS ALTITUDE**

#### Bullock and Rayburn, 1991; McMurphy and Rayburn, 1992

The same forces affecting DNA content between species are also active within a species.

Looked at DNA content of maize adapted to different regions of Arizona and New Mexico

Found a correlation between DNA content and altitude, probably attributable to a correlation between DNA content and growing degree days (a measure of the length of the growing season)

The longer the growing season, the more time available for reproduction, and the greater amount of DNA



Decrease occurred in C-band heterochromatin, consisting of

- knobs seen at chromosome ends at meiosis
- repetitive heterochromatic DNA

#### TALL FESCUE IN ITALY

#### Ceccarelli et al, 1992

A similar relationship has been found in tall fescue from different parts of Italy



In general, studies do not agree on the effect of environment on DNA content

The table summarizes the seemingly contradictory associations found between DNA content and environmental factors:

#### Knight et al., 2005

Variable	+ Correlation to 2C DNA Content	- Correlation to 2C DNA Content	Non-linear or Non- significant Correlation
Altitude	8	9	7
Latitude	5	8	6
Temperature	4	9	2
Precipitation	4	3	1
Seed Mass	11	0	1
Generation Time	12	3	4
Relative Growth Rate	5	4	2

#### **Measurement errors**

#### **Greilhuber 2005**

Premise is that most estimates of DNA content variation are wrong:

Lack of an internal standard in flow cytometry and DNA staining with propidium iodide lead researchers to conclude that Chinese soybean (*Glycine max*) accessions varied greatly in their genome size (filled columns)

But a re-investigation with an internal standard in flow cytometry and Feulgen densitometry showed only minor variation (open columns). Greilhuber 2005 data in grey, super-imposed on Rayburn data (black)



#### VII-C - Changes in DNA content PBGG 8900 Spring 2025 | page 29 Rayburn et al, 2004

Since Greilhuber's results suggested that intraspecific variation did not exist in soybean, **Rayburn et al.** (2004) published a follow-up paper, using an internal standard and various other controls, documenting the existence of intraspecific variation:

Line	# Plants	Relative mean	Standard deviation
PI 266085	22	2.847	0.093
PI 227324	22	2.825	0.064
PI 437088	22	2.814	0.071
PI 253666	22	2.814	0.076

DNA amount difference between high and low lines amounted to approximately 1%

- The experiments in that paper showed differences of up to 4%
- Since soybean has over 2 billion base pairs of DNA per 2C, this 1 to 4% variation in genome size translates to a difference of 11 to 45 million base pairs per 1C genome

# **DNA content vs invasiveness**

#### Rejmánek, 1996 Review by Suda et al, 2014

First to associate low DNA content with invasiveness (Z score) in pine and other spp.





#### Reed canarygrass Lavergne et al., 2010

Highly invasive genotypes of reed canarygrass have lower DNA content:



Average DNA content of invasive and non invasive genotypes



Correlation between stem growth rate and DNA content. These parameters were not significantly correlated in native (non invasive) genotypes, but very negatively correlated with invasive genotypes.

# **DNA content vs rise of angiosperms**

#### Simonin & Roddy, 2018

In angiosperms, genome downsizing (determined by measuring stomatal guard cell size in fossils) was accompanied by increased vein density and stomatal density.

• Less DNA = smaller cells = greater surface to volume ratio = better ability to absorb CO<sub>2</sub> from the air



*Right: Regression between genome size and stomatal conductance, plotted on a log-log scale. Assumptions of three leaf thicknesses (70, 100, 130 \mum,) and an assumed vapor pressure deficit of 2 kPa. F = ferms; G = gymnosperms; A = Angiosperms* 

# DNA content vs life cycle

#### Swanson, Merz, & Young, 1981

There is a strong relationship between DNA content and growth habit (i.e., annual versus perennial).

DNA content, duration of mitosis, duration of meiosis, and growth habit in several plant species:

Species	pg/haploid genome	Mitosis (hours)	Meiosis (hours)	Plant habit
Crepis capillaris	1.20	10.8		Annual
Haplopappus gracilis	1.85	10.5	36.0	Annual
Pisum sativum	3.9, 4.8	10.8		Annual
Ornithogalum virens	6.43		96.0	Perennial
Secale cereale	8.8, 9.6	12.8	51.2	Annual
Vicia faba	13.0, 14.8	13.0	72.0	Annual
Allium cepa	14.8, 16.25	17.4	72.0	Perennial
Tradescantia paludosa	18.0	18.0	126.0	Perennial
Endymion nonscriptus	21.8		48.0	Perennial
Tulipa kaufmanniana	31.2	23.0		Perennial
Lilium longiflorum	35.3	24.0	192.0	Perennial
Trillium erectum	40.0	29.0	274.0	Perennial



Note differing DNA contents for some species. These discrepancies due to:

- Method used (flow cytometry is considered the most accurate)
- Naturally occurring intraspecific variability

#### Definitions

#### Bennett 1987

- Annual
  - o Sets seed and completes life cycle within one year (52 weeks) or less
  - Hence, a fast growth rate is essential
- Perennial
  - o Does not complete life cycle within 1 year
- Facultative perennial
  - Sets seed within 1 year
- Nucleotypically determined obligate perennial
  - The DNA content slows down the cell cycles to where the plant cannot set seed or complete its life cycle within one year
- Genotypically determined obligate perennial
  - o Long life cycle not determined by DNA content, such as juvenility in trees
- Temperature-determined obligate perennials
  - o Extreme environments with growing seasons too short to complete a life cycle in 1 year

#### Effect of DNA @ constant temperature Bennett, 1987

In a temperate climate, DNA content can determine growth habit.

Generation time controlled by DNA amount

Line AD = shortest generation time for a given amount of DNA

Obligate perennials have too much DNA to complete their life cycle within a 52-week (i.e, 1 year) period



#### Effect of DNA considering temperature Bennett, 1987

When climate becomes a variable, it interacts with DNA content to determine growth habit.

All angiosperms are below the plane defined by ADZY

As temperature drops, the maximum DNA content also drops.

Therefore, it is not possible to have rapid cycling plants below X'

Below Y, only obligate perennials are possible



Minimum generation time

Category of Plant	DNA C-value is below the segment:	Minimum generation time is:	The plants can exist at temperatures:
Ephemerals	AB	≤ <mark>7 weeks</mark>	>X′
Annuals and Facultative Perennials	BC	≤52 weeks but >7 weeks	>Y′
Genotypically- determined obligate perennials	C	>52 weeks	>Y′
Nucleotypically- determined obligate perennials	CD	>52 weeks	>Y′
Temperature-determined obligate perennials	can be as great as CD but tends to be lower	>52 weeks	<y′< td=""></y′<>