The scaling of genome size and cell size limits maximum rates of photosynthesis with implications for ecological strategies

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Abstract

A central challenge in plant ecology is to define the major axes of plant functional variation with direct consequences for fitness. Central to the three main components of plant fitness (growth, survival, and reproduction) is the rate of metabolic conversion of CO_2 into carbon that can be allocated to various structures and functions. Here we (1) argue that a primary constraint on the maximum rate of photosynthesis per unit leaf area is the size and packing density of cells and (2) show that variation in genome size is a strong predictor of cell sizes, packing densities, and the maximum rate of photosynthesis across terrestrial vascular plants. Regardless of the genic content associated with variation in genome size, the simple biophysical constraints of encapsulating the genome define the lower limit of cell size and the upper limit of cell packing densities, as well as the range of possible cell sizes and densities. Genome size, therefore, acts as a first-order constraint on carbon gain and defines the upper limits of allocation to growth, reproduction, and defense. The strong effects of genome size on metabolism, therefore, have broad implications for plant biogeography and for other theories of plant ecology.

Introduction

Quantifying major axes of plant functional variation has given rise to an ever-growing list of traits that impact growth, reproduction, and survival, the three components of individual fitness (Violle et al. 2007). These traits have traditionally been viewed from a reductionist perspective that scales form-function relationships of individual plant organs, e.g. leaves, stems, and roots, to whole organism ecological strategies. As the ultimate source of energy and matter for growth and reproduction, photosynthetic capacity represents a first-order constraint on the emergent properties between whole plant form and function and individual fitness. Here we provide evidence that genome-cellular allometry directly influences interspecific variation in photosynthetic metabolism and provide a mechanistic framework that links genome size and metabolism to other aspects of plant ecology and evolution.

A major limitation on photosynthetic capacity is the ability to deliver resources to, and exporting products from, the sites of metabolic processing (Enquist et al. 1998; West et al. 1999a; Brown et al. 2004). At the level of an individual cell–the fundamental unit of living organisms–rates of resource transport are strongly influenced by cell size because the ratio of cell surface area to cell volume increases exponentially with decreasing cell size. Building on an extensive body of literature we show how variation in the size of the nuclear genome fundamentally limits the sizes and packing densities of cells, and, as a result, the maximum rate of photosynthetic metabolism across vascular plants.

One of the three components of fitness is growth which is ultimately limited by photosynthetic capacity. Relative growth rate (RGR) varies considerably across species and is driven by photosynthetic rate and the resource investment to support photosynthesis as:

$$RGR = A_{mass} \cdot LMR$$

where A_{mass} is the photosynthetic rate per unit leaf biomass and LMR is the leaf mass ratio (the proportion of leaf dry mass to total plant dry mass). A_{mass} is, therefore, frequently

considered a major plant strategy axis (Poorter and Remkes 1990; Poorter et al. 1990; Reich et al. 1992). However, A_{mass} can be decomposed as:

$$A_{mass} = SLA \cdot A_{area}$$

where SLA is the specific leaf area (leaf area per leaf dry mass) and A_{area} is the net carbon assimilation rate per unit canopy leaf area. Because of its direct effect on A_{mass}, SLA is often considered a major predictor of interspecific variation in RGR. A_{area}, on the other hand, varies orthogonally to SLA (Wright et al. 2004), and, therefore, determines the upper limit of the relationship between A_{mass}, SLA, and RGR. Maximum potential A_{area} represents, then, a fundamental limitation on the maximum amount of carbon available for allocation to growth, reproduction, and survival relative to species ecological strategies. The centrality of A_{area} to plant ecological strategy suggests two questions:

- First, what are the fundamental features of plant structure that determine maximum potential A_{area}?
- Second, to what extent do these relationships scale up to affect plant ecological strategies and evolutionary dynamics?

Here we present a mechanistic framework to address both of these questions, that is based on a long-recognized but often overlooked relationship: positive scaling between genome size and cell size. Although the relationship between genome size (i.e. nuclear volume) and cell size has long been of interest (Sachs 1893), the mechanisms are still not fully understood (Doyle and Coate 2019). Yet, we show that the allometry between genome size and cell size directly influences rates of photosynthetic metabolism and argue that the scaling of genome size and metabolism affects ecological distributions and evolutionary dynamics. In this way, any factor affecting rates of metabolism is a potential agent of selection on the genome, if only via selection on genome size.

It is now widely recognized that variation in genome size can have significant consequences for organismal structure and function, independent of the genes that define the genotype (Bennett 1971). Positive scaling between genome size and cell size across terrestrial plants has given rise to numerous studies characterizing the many other

95 phenotypic correlates of genome size independent of variation in genome structure,
96 commonly referred to as "nucleotype" effects (Bennett 1971; Cavalier-Smith 1978; 1982;
97 Bennett and Leitch 2005). Correlates of genome size encompass an incredible diversity of
98 plant phenotypes, including, for example, the sizes of plant structures, rates of cell division,
99 rates of physiological processes, and tolerances and responses to abiotic conditions (Table
100 1).

101 Our goal is not to recapitulate the many reviews about the nucleotype-phenotype
102 relationship but, instead, to align these studies more systematically with the field of plant
103 functional biology. We believe that the diverse impacts of genome-cellular allometry on the
104 body plan of terrestrial vascular plants strongly influences the coordination between plant
105 functional traits and, ultimately, whole organism form-function relationships. Here we
106 summarize previous research, perform new analyses of existing data, and present new data
107 to show how genome size may, through its impacts on cell size and tissue structure,
108 determine the biophysical limits of plant metabolic rates, and, therefore, influence other
109 aspects of ecology and evolution. That genome size may be a key functional trait is not a
110 new idea (Grime 1998). Yet, despite numerous reports of the phenotypic and ecological
111 correlates of genome size (Table 1), it has not been fully identified and integrated into the
112 functional trait literature. Our goal, therefore, is to more directly show how genome size
113 influences plant traits that impact maximum rates of photosynthetic metabolism.
114 Metabolism is central to all three aspects of plant fitness, providing the carbon necessary
115 for allocation to growth, reproduction, and survival. As such, genome size may not itself be
116 a functional trait but instead may define the limits of variation in numerous other
117 functional traits.

118 Genome-cellular allometry limits rates of resource transport and 119 metabolism

120 Allometry of genome size and cell size

121 The role of the genome in limiting cell size has been postulated since at least the late 1800s
122 (Sachs 1893) and was critical in shaping early modern views of the evolution of plant

vascular systems (Bailey and Tupper 1918). At a minimum, a cell must contain its genome, and there is a strong relationship between the volumes of meristematic cells and genome size (Šímová and Herben 2012). Cellular expansion from this meristematic minimum size is cell type-specific (Doyle and Coate 2019). Within a cell type, size can be influenced by various environmental and developmental factors (Melaragno et al. 1993). Despite this substantial growth in cell volume during development, there remains a significant effect of genome size on cell size, particularly for stomatal guard cells (Beaulieu et al. 2008; Knight and Beaulieu 2008; Lomax et al. 2013; Simonin and Roddy 2018). For example, stomatal guard cell size and density, which regulate the fluxes of water and CO_2 between the biosphere and atmosphere, vary within species depending on light, water availability, and atmospheric CO_2 concentration (Hetherington and Woodward 2003; Franks and Beerling 2009). Furthermore, in the vascular transport network, the sizes of xylem conduits and their density in the leaf are also affected by variation in genome size (Maherali et al. 2009; Hao et al. 2013; De Baerdemaeker et al. 2018; Simonin and Roddy 2018). Yet why genome size and final cell size are correlated within a cell type remains unclear (Doyle and Coate 2019).

We tested whether smaller genomes allow not only for smaller initial and final cell sizes but also for a greater range in final cell size using published data for terrestrial C3 plants. We used data for stomatal guard cells because they are the most commonly measured cell sizes in plants and because their sizes and abundance determine the leaf surface conductance to CO_2 and water vapor and, therefore, directly control rates of resource transport for use in photosynthetic metabolism. Sizes of guard cells for angiosperms (Beaulieu et al. 2008), gymnosperms, and ferns were compiled previously by Simonin and Roddy (2018), and here we include data for mosses and hornworts from Feild et al. (2015) and Renzaglia et al. (2017). We assumed that stomatal guard cells are shaped as capsules, which are composed of a central cylinder with hemispherical ends, such that cell volume could be estimated from cell length as:

$$\boxed{V = \pi \cdot r^2 \cdot (\frac{4}{3} r + a)}$$

151 where r is the radius of the cylinder and a is the height of the cylinder. We assumed that a
152 is equal to $2r$. The dumbbell-shaped guard cells common among grasses would likely
153 violate these assumptions about cell shape and so we have not included in this analysis
154 data for lineages known to have dumbbell-shaped guard cells. Data for meristematic cell
155 volume and genome size were taken from Simova and Herben (2012). We used standard
156 major axis regression (R package *sma*) to fit the mean response and quantile regression (R
157 package *rq*) to test whether there was greater variation in cell volume among taxa with
158 smaller genomes (i.e. heteroskedasticity).

159 For a given genome size, mature guard cells were at least three orders of magnitude more
160 voluminous than meristematic cells (Figure 1). Genome size was a strong and significant
161 predictor of meristematic cell volume (log(volume) = 1.24 log(genome size) - 0.23; R^2 =
162 0.98, P < 0.001; Šímová and Herben 2012). Though it explained less of the variation,
163 genome size was a significant predictor of final guard cell volume (log(cell volume) = 0.80
164 log(genome size) + 3.43; R^2 = 0.09, P < 0.001). Quantile regression revealed that the slope
165 through the 10% quantile was steeper (0.58) than the slope through the 90% quantile (-
166 0.07), reflecting both the greater variation in final cell volume among species and the
167 smaller minimum possible cell volume that can be obtained with smaller genomes
168 (i.e. heteroskedasticity in cell volume with variation in genome size). Thus, smaller
169 genomes allow for smaller minimum cell size with little or no effect on maximum cell size,
170 together enabling greater potential variation in final cell size. The greater variation among
171 species with smaller genomes implies that smaller genomes allow for greater plasticity in
172 cell sizes and cell packing densities which directly influence maximum rates of leaf surface
173 conductance to CO_2 and water and ultimately photosynthetic metabolism per unit leaf
174 surface area (Simonin and Roddy 2018). Further, the greater diversity of cell sizes
175 observed in plants with small genomes is supporting evidence that the correlation between
176 genome size and cell size is simply the result of occupying available space within the cell. A
177 small genome can be housed in either a small or a large cell, but a large genome requires a
178 cell large enough to contain its volume.

179 The greater variation in cell volume allowed by smaller genomes across terrestrial C3
180 plants (Figure 1) further suggests that smaller genomes allow for greater variation in cell

181 packing densities. For guard cell lengths, stomatal densities, and vein densities, smaller
182 genomes allowed for greater variation in traits across ferns, gymnosperms and
183 angiosperms (Simonin and Roddy 2018). Species with smaller genomes in these datasets
184 are predominantly angiosperms, and these analyses compared distantly related species.
185 We further tested for greater variation in cell sizes and packing densities with smaller
186 genomes among closely related species using taxa in *Rhododendron* sect. *Schistanthe* Schltr.
187 (= sect. *Vireya* Blume). This monophyletic clade has a stepwise phylogeographic history,
188 having radiated eastward from the Malay Peninsula and reached New Guinea within the
189 last 15 Ma (Goetsch et al. 2011). We sampled leaves from 19 taxa growing under common
190 garden conditions at the Rhododendron Species Foundation Botanical Garden in Federal
191 Way, WA, USA. Genome sizes were measured following standard protocols (Dolezel et al.
192 2007) at the Benaroya Research Institute in Seattle, WA, USA. For measurements of
193 stomatal size and density, epidermal impressions were made on fresh leaves using dental
194 putty (Coltene Whaledent President Light Body), transferred using clear nail polish,
195 mounted in water, and imaged using a light microscope. Measurements of leaf vein density
196 were made on leaf sections cleared by soaking in 4% NaOH, 3% sodium hypochlorite,
197 stained with 1% Safranin O, counterstained with 1% Fast Green, mounted in ethanol, and
198 imaged with a light microscope. Stomatal traits were averaged across ten images per taxon,
199 and leaf vein density was averaged across five images per taxon. Quantile regression (R
200 package 'rq') through the 10th and 90th percentile of the species means were used to
201 quantify the variation in traits associated with variation in genome size. Consistent with
202 previous results across vascular plants (Simonin and Roddy 2018), among the closely
203 related *Rhododendron* sect. *Schistanthe*, there was greater variation in the sizes and packing
204 densities of veins and stomata among species with smaller genomes (Figure 2).
205 Furthermore, the steeper quantile slopes for the lower limit of cell size and the upper limit
206 of packing densities are consistent with the hypothesized constraints imposed by genome
207 size variation.

208 **Genome size limits maximum photosynthetic metabolism**

209 Previous work has hypothesized that genome size would be linked to maximum
210 photosynthetic rate but found little support (Knight et al. 2005; Beaulieu et al. 2007). We

211 hypothesize that one major reason for not finding support is that these previous studies
212 attempted to predict variation in A_{mass}, which accounts for the construction costs of leaves,
213 rather than A_{area}, which is the maximum metabolic rate regardless of the construction costs.
214 As we described above, A_{area} would define the maximum amount of carbon assimilated, but
215 how the plant allocates the total assimilated carbon–to growth, reproduction, defense,
216 more durable leaves, etc. (Bazzaz et al. 1987)–would reflect the numerous factors that
217 influence plant form and other aspects of plant function. Thus, A_{area}, which is orthogonal to
218 SLA and A_{mass} (Wright et al. 2004), is predicted to be constrained by cell and genome sizes.
219 Consistent with this prediction, recent work has shown that genome size is a strong
220 predictor of the sizes and densities of stomatal guard cells and leaf veins across vascular
221 plants (Simonin and Roddy 2018), and we predicted, therefore, that genome size would, via
222 its effects on the sizes and packing densities of cells, predict A_{area}.

223 Data for area-based maximum photosynthetic rate were compiled from the primary
224 literature (Supplemental Table 1) and merged with the Kew Plant DNA C-Values Database
225 (Bennett and Leitch). This dataset included 210 species, of which 138 were angiosperms,
226 46 were gymnosperms, and 26 were ferns. We tested for a relationship between genome
227 size and A_{area} both for the mean response (standard major axis regression, SMA; R package
228 'smatr') and for the upper 90% quantile of the data using quantile regression (R package
229 *rq*). To test whether the SMA regression was driven by phylogenetic history, we used a
230 phylogenetically corrected version (R package 'phytools'), which provides a P-value only
231 for the test against a specific slope, for which we used the non-phylogenetically corrected
232 SMA slope. For this analysis, we generated a dated supertree using the methods of Simonin
233 and Roddy (2018), which included generating a family-level supertree using the R package
234 'brranching' (Chamberlain 2016) and applying node ages from Magallón et al (2015). Of the
235 128 nodes, 43 with node names had ages. These ages were applied and intermediate
236 branch lengths smoothed using 'bladj' in Phylocom (Webb et al. 2008). We randomly
237 resolved polytomies by adding 5 million years to each branch and subtracting an
238 equivalent amount from the subtending branches to keep the tree ultrametric.

239 Species with smaller genomes had higher maximum photosynthetic rates across and within
240 major plant clades (Figure 3). Standard major axis regression on log-transformed data

241 revealed a significant negative relationship between genome size and A_{area} across all
242 species (log(A_{area}) = -0.42 log(genome size) + 1.29; R^2 = 0.23, P < 0.001). The phylogenetic
243 major axis regression was significantly steeper than the non-phylogenetic major axis
244 regression (log(A_{area}) = -0.75 log(genome size) + 1.76; slope test P < 0.001), suggesting that
245 the evolution of genome size across land plants is strongly associated with changes in A_{area}
246 across vascular plants. A similarly negative relationship was apparent among the upper
247 (90%) quantile, which showed that A_{area} was lower among species with larger genomes.
248 Despite the large difference in genome size between angiosperms and gymnosperms, the
249 90% quantile regression slopes were nearly identical for the entire dataset (-0.19) as for
250 the angiosperms alone (-0.18).

251 The scaling relationship between A_{area} and genome size follows naturally from the
252 relationships between genome size and the sizes and densities of veins and stomata.
253 However, veins and stomata are not the only cells responsible for driving variation in
254 photosynthetic rates. While the maximum rate of CO_2 diffusion into the leaf is defined by
255 the sizes and densities of stomata (Franks and Beerling 2009), once inside the leaf, CO_2
256 must diffuse through the leaf intercellular airspace and into the chloroplasts lining the
257 interior surfaces of mesophyll cells. The diffusive surfaces of the leaf mesophyll are the
258 interface between liquid-phase and vapor-phase resource movement, where liquid water
259 delivered by the veins evaporates and where CO_2 must diffuse into the liquid phase. Thus,
260 the three-dimensional structure and organization of the mesophyll is predicted to be a
261 prime target for selection on photosynthetic metabolism (Tholen et al. 2012; Ren et al.
262 2019) and to be critical to leaf photosynthetic function (Earles et al. 2019), and the limited
263 evidence on *Arabidopsis thaliana* mutants with altered cell diameter and porosities point in
264 that direction (Lehmeier et al. 2017). We predict, therefore, that the scaling relationships
265 between genome size and cell size that coordinate veins and stomata (Simonin and Roddy
266 2018) extend also to the photosynthesizing cell size, structure, and organization within the
267 leaf mesophyll. The significant negative scaling relationship between A_{area} and genome size
268 would emerge from the effects of genome size on the sizes and packing densities in each of
269 these tissues.

Genome size limits the rate of metabolic up- or down-regulation

Although maximum potential rate of leaf gas exchange is an important parameter determining a species' physiological capacity, the actual rate of leaf gas exchange at any given moment is often substantially lower, depending on a variety of physiological and environmental factors (e.g. light level, atmospheric humidity, leaf temperature, plant water status). Changes in sun angle, shading by passing clouds, and self-shading by fluttering leaves all drive changes in incoming solar radiation, and these rapid dynamics have influenced the evolution of photosynthetic biochemistry (Pearcy 1990). Under naturally varying conditions, leaf gas exchange fluctuates dramatically and rarely reaches its maximum rate, with greater variation occurring at the top of the plant canopy. How frequently a leaf can reach its maximum gas exchange rate and how well optimize its physiological processes to environmental conditions depend on how rapidly the leaf can respond to dynamic, fluctuating conditions.

An emerging consensus is forming that smaller stomata respond more rapidly to fluctuating conditions than larger stomata, allowing leaves with smaller stomata to more closely tune their physiological rates with environmental conditions (Drake et al. 2013; Lawson and Blatt 2014; Lawson and Vialet-Chabrand 2019). Leaf physiological processes change at different rates, with changes in stomatal conductance occurring an order of magnitude more slowly than changes in photosynthesis (McAusland et al. 2016). This difference in response times between physiological processes (e.g. photosynthetic assimilation rate and stomatal conductance) can reduce water use efficiency when stomata are closing and reduce photosynthetic efficiency when stomata are opening (Lawson and Vialet-Chabrand 2019), limiting total photosynthesis by up to 20% (Lawson and Blatt 2014). If stomatal response times are directly limited by the size of stomata then genome-cellular allometry fundamentally limits not only the maximum rate of metabolism but also how quickly metabolism can respond to environmental change. Of the species for which stomatal response times were measured by McAusland et al. (2016) and Drake et al. (2013), twelve were included in the Kew Plant DNA C-Values database. Consistent with previous reports, there was a positive correlation between genome size and guard cell length (Figure 4a), and stomatal response rate exhibited a triangular relationship with

genome size such that smaller genomes exhibited both higher maximum stomatal response rates but also a greater variation in stomatal response rate. While the available data on stomatal response rates measured using standard protocols are limited, these preliminary results suggest that genome size indirectly limits the maximum rate of stomatal opening and closing via its effects on the sizes and densities of stomata.

Implications of genome size-metabolism scaling on plant biogeography

Polyploidy thought to increase habitat breadth

Variation in genome size and structure associated with polyploidization has long been considered to be an important driver of plant evolution and to be associated with environmental tolerances, habitat breadth, trait variation, and interspecific interactions (Stebbins 1940; Otto and Whitton 2000; Soltis et al. 2003; Soltis et al. 2014; Michael S Barker et al. 2016; 2016), all of which influence species biogeography. Describing the types of polyploids and how they are generated is outside the scope of the current manuscript and have been thoroughly reviewed elsewhere (e.g. Stebbins Jr 1947; Soltis et al. 2015). Rather, we focus our discussion here on how and why ploidy–via its relationship with genome size–may or may not correlate with species distributions and habitat breadth.

Polyploids have been hypothesized to be better adapted to extreme habitats, to have greater hardiness, and to have greater ecological adaptability [reviewed by (Stebbins 1985: @Brochmann:2004aa). The possible mechanisms for these effects can be roughly grouped into two categories: one involving the genetic and genic content of the polyploid genome and one involving the nucleotypic effects of ploidy and genome size. Because polyploid genomes have additional genome copies, they have higher absolute genic contents, would enable neofunctionalization of duplicated genes, and typically have higher heterozygosity, all of which can promote higher tolerances of environmental conditions. The nucleotypic effects of ploidal variation, though long recognized (Stebbins 1940), are often confounded with nucleotypic effects of genome size variation.

327 While ploidy and genome size are commonly assumed to be synonymous, at broad
328 phylogenetic scales there is frequently no relationship between genome size and ploidy
329 (Leitch and Bennett 2004), reflecting the complex history of both ancient and
330 contemporary whole genome duplications, particularly among the angiosperms (Jiao et al.
331 2011; Clark and Donoghue 2018; Landis et al. 2018; Ren et al. 2018). Angiosperm genomes
332 readily rediploidize after polyploidization such that genome size and ploidy are positively
333 correlated only for narrowly defined phylogenetic groups (i.e. within genera and families,
334 Figure 5; Leitch and Bennett 2004; Dodsworth et al. 2016). Ferns, by contrast, the other
335 major group of vascular plants that readily undergoes polyploidization events seem not to
336 rediploidize as readily (Clark et al. 2016), as evidence by the positive correlation between
337 genome size and ploidy (Figure 5). If leaf and plant structure and function influence
338 ecological tolerances and habitat breadth (i.e. if plant structure-function is adaptive), then
339 the nucleotypic effects of genome size are predicted to influence environmental tolerances.

340 ### Smaller genomes enable greater phenotypic plasticity

341 One long-standing hypothesis is that higher ploidy is related to wider habitat breadth
342 because polyploids can tolerate greater ecological stress. Higher ploidy is associated with
343 greater heterozygosity (i.e. greater genetic diversity) and, frequently, higher genic content
344 due to multiple genome copies, both of which are thought to promote plasticity and enable
345 polyploids to withstand a greater range of environmental conditions than diploids.
346 However, several studies testing this hypothesis have not observed polyloids to have
347 greater habitat breadth (e.g. Stebbins 1985; Martin and Husband 2009; Johnson et al.
348 2014). Furthermore, these tests frequently find that diploids exhibit greater habitat
349 breadth than polyploids (Petit and Thompson 1999; Hijmans et al. 2007; Brittingham et al.
350 2018). One reason is that traits of polyploids are not necessarily more variable than in
351 diploids (Stebbins 1985; Wei et al. 2018).

352 We predict that one reason ploidy is not commonly found to correlate with ecological
353 breadth is because genome size–rather than ploidy per se–drives variation in the absolute
354 range of potential cell sizes and, by extension, phenotypic plasticity in rates of resource
355 transport and metabolism. Thus, the phylogenetic scale-dependence of the relationship

356 between genome size and ploidy could lead to confounding patterns depending on the
357 phylogenetic scale at which comparisons are made. For example, in the analysis of Rice et
358 al. (2019), ploidy was determined relative to other closely related species, such that within
359 genera or families ploidy and genome size are positively correlated, suggesting that the the
360 bias towards higher abundances of polyploids at higher latitudes may reflect nucelotypic
361 effects of genome size on cell size and metabolism. The complex, fluctuating process of
362 polyploidization and rediploidization, which can winnow the genome nonrandomly
363 (Wendel 2015), would promote the proliferation of beneficial elements associated with
364 genome duplications (e.g. more gene copies that can neofunctionalize) while reducing the
365 size of the genome needed to maintain high rates of development and metabolism (Table
366 1).

367 We posit here that the nucleotypic effects of genome size, regardless of ploidy, may
368 influence environmental tolerances. Because smaller genomes allow for greater variation
369 in cell size (Figure 1), species with smaller genomes may be better able to fine tune their
370 tissue structure to environmental conditions. This flexibility would allow species with
371 smaller genomes to better optimize their metabolic rates in order to occupy a wider range
372 of environmental conditions. Combined with the effects of genome size on rates of cell
373 division (Van't Hof and Sparrow 1963; Hof 1965; Šímová and Herben 2012), the greater
374 plasticity in cell size and higher rates of maximum photosynthesis available to species with
375 small genomes may enable them to better colonize new habitats.

376 **Greater variation in genome size in less productive habitats**

377 In habitats that can support high rates of productivity and primary metabolism, species
378 with small genomes are expected to predominate. At a broad scale, this prediction holds
379 because angiosperms, which have, on average, smaller genomes than other vascular plants
380 are dominant in most ecosystems, particularly those characterized by high productivity.
381 However, high rates of metabolism, even among the angiosperms, are not always favorable.
382 Two such habitats are those characterized by extreme water limitation and nutrient
383 limitation, such as deserts and epiphytic habitats, and by extreme cold, such as high
384 latitudes. Higher incidences of polyploids have been commonly reported in higher latitudes

385 and among arctic floras (Brochmann et al. 2004; Rice et al. 2019), but arid habitats have
386 received less attention.

387 Arid and epiphytic habitats are characterized by low productivity and may support species
388 with large genomes. In these habitats, high rates of metabolism are not always favored,
389 which may relax selection for small genomes. One strategy common in arid and epiphytic
390 habitats is succulence, which is often associated with Crassulacean acid metabolism (CAM)
391 photosynthesis. The CAM syndrome limits water loss by sequestering CO_2 uptake and
392 water loss to nighttime which corresponds with periods of concomitant water loss to
393 periods of high humidity and little energy available to drive water loss (i.e. at night). As a
394 result, this strategy is characterized by low rates of resource transport. If metabolism is
395 one axis of selection on genome size, then we would predict that CAM species may,
396 therefore, have larger genomes than species employing C3 metabolism. We tested this
397 hypothesis using the taxonomic distributions of CAM photosynthesis from Smith and
398 Winter (1996) and genome size data from the Kew Plant DNA C-Values Database (citation).
399 For C3, we used the broad distribution of angiosperms reported in Simonin and Roddy
400 (2018), which are representative of extant angiosperm diversity. We scored as CAM the
401 narrowest taxonomic level in the Kew DNA C-Values Database that was listed as containing
402 CAM by Smith and Winter (1996). For example, if a genus were listed as containing any
403 CAM species, all species in the genus were assumed to exhibit CAM photosynthesis. This
404 strategy was biased against observing differences in genome size between C3 and CAM
405 species because it necessarily grouped some C3 species as CAM. Nonetheless, genome sizes
406 were significantly larger among CAM species than among C3 species even after log-
407 transforming the data to improve normality (t-test: $t = 9.72$, $df = 272.6$, $P < 0.0001$; Figure
408 6), consistent with the prediction that large genomes may evolve when selection for high
409 rates of metabolism is weak.

410 Arid habitats are not exclusively composed of species with large genomes. Rather, they may
411 harbor a diversity of strategies associated with divergent niches. While many C3 species in
412 deserts function during a relatively narrow window in the year, either because they are
413 annuals or because physiological activity in perennial shrubs is restricted to a narrow
414 range of environmental conditions, when water is available. Thus, because their carbon

415 gain is limited to such a short time period, they may have small genomes and cells that
416 enable high rates of metabolism. Desert shrubs have the highest rates of stem hydraulic
417 conductance measured in C3 plants (Mencuccini 2003), and even among species from
418 humid tropical forests, dry forest species have higher hydraulic conductance than wet
419 forest species (Brenes-Arguedas et al. 2013). Thus, less productive habitats may allow for
420 multiple strategies that encompass a broader range of metabolic rates and, allowing for
421 greater variation in genome size at the community level than might be observed in
422 conditions more favorable to high rates of metabolism and productivity.

423 **Smaller genomes increase the probability of invasiveness**

424 The multifaceted effects of genome size on plant structure, function, and ecology (Table 1)
425 is particularly relevant to the study of invasive species. Identifying the traits that allow an
426 introduced species to establish, naturalize, and invade into a new environment is a central
427 aim of invasion biology (Simberloff 2011), with broader implications for plant
428 biogeographic patterns. Here we distinguish between nonnative species–those that survive
429 and reproduce in their introduced range–and nonnative invasive species–those that can
430 disperse and establish far from their original source of introduction (Richardson et al.
431 2011). This distinction is important because prior studies on the traits of 'invaders' focus
432 on these different subsets of species, which have slightly different, but overlapping, sets of
433 traits that determine whether they can survive and reproduce versus invade (Kleunen et al.
434 2015).

435 Early theory on the distinguishing traits of invasive plants postulated that "ideal weeds"
436 should grow rapidly, produce seed continuously and in high number throughout the
437 growing season, be tolerant to a wide range of environmental conditions, exhibit high trait
438 plasticity, and be able to reproduce vegetatively from fragments (Baker 1974). On average,
439 these predictions have been upheld, with nonnative invasive plants tending to exhibit traits
440 consistent with high fitness (e.g., number of flowers, fruits, or seed or germination rates),
441 high relative growth rates, high dispersal abilities (smaller seeds), and more efficient
442 carbon-capture strategies (e.g. high specific leaf area), relative to co-occurring native
443 species (Leishman et al. 2007; Kleunen et al. 2010; Ordonez et al. 2010; Kuester et al. 2014)

444 or naturalized but not invasive nonnative species (Rejmánek and Richardson 1996;
445 Gallagher et al. 2014). Combined, these traits confer a growth advantage, such that plants
446 with small seeds can disperse further distances, have shorter generation times, and higher
447 relative growth rates, owing to the greater rates of cell division and higher metabolic rates
448 provided by smaller genomes (Pandit et al. 2014; Suda et al. 2015). Indeed, even within
449 species, populations with smaller genomes are more likely to successfully invade new
450 habitats (Pysek et al. 2018).

451 Because many of the traits linked with invasiveness can be influenced by both ploidy and
452 genome size, both have been implicated as underlying features driving invasion (Pandit et
453 al. 2014; Suda et al. 2015). Because polyploids are thought to be better able to tolerate
454 environmental fluctuations and to be better able to adapt to new environments, polyploids
455 tend to be overrepresented among nonnative invasives compared to native angiosperms
456 (Rejmánek and Richardson 1996; Prentis et al. 2008; Beest et al. 2011; Pandit et al. 2014).
457 Similarly, nonnative invasive species tend to have smaller genomes than non-invasive
458 plants (both native and non-native), which is thought to be due to the diverse effects of
459 genome size on metabolism, rates of development and growth, and seed size (Rejmánek
460 and Richardson 1996; Bennett et al. 1998; Kubešová et al. 2010; Pandit et al. 2014).
461 However, the complex, scale-dependent relationship between ploidy and genome size
462 discussed previously complicate a clear understanding of the effects of ploidy versus
463 genome size on invasiveness (Rejmánek and Richardson 1996; Pandit et al. 2014). Because
464 angiosperms, which predominate among nonnative invasives, readily rediploidize and
465 downsize their genomes subsequent to whole genome duplications (Leitch and Bennett
466 2004), assessing the relative effects of ploidy versus genome size on invasiveness can be
467 difficult. For example, the likelihood of being invasive increases with chromosome number
468 and ploidy but decreases with genome size (Rejmánek and Richardson 1996; Pandit et al.
469 2014). The multiple paths to polyploidization and the selective retention of only certain
470 parts of the genome during subsequent genome downsizing (Wendel 2015) could explain
471 how both higher ploidy and smaller genomes are correlated with invasiveness.

472 ## Implications for of genome size variation on the Metabolic Theory of
473 Ecology

474 As the major source of energy and matter for the biosphere, photosynthetic metabolism
475 represents a first-order control over ecological processes globally. This fundamental link
476 between metabolic and ecological processes has driven the development of the Metabolic
477 Theory of Ecology (MTE) that provides a mechanistic framework for predicting variation in
478 organismal life history attributes, population dynamics, and larger scale ecosystem
479 processes from organismal-level traits related to supplying resources for metabolism
480 (West et al. 1997; Enquist et al. 1998; West et al. 1999a; West et al. 1999b; West et al. 2002;
481 Price et al. 2010). While appealing and seemingly endowed with incredible explanatory
482 power, a number of criticisms of the theory and its assumptions have been consistently
483 raised (Kozłowski and Konarzewski 2004; Kozłowski and Konarzewski 2005; Price et al.
484 2012). One primary assumption is that the sizes of terminal units in vascular networks
485 (e.g. capillaries in circulatory systems or terminal veins in plant leaves) are invariant. The
486 problems with this assumption have been thoroughly detailed for animal circulatory
487 systems with the allometry of genome size and cell size emerging as a critical factor
488 influencing how body size scales with metabolism (Kozłowski et al. 2003). Furthermore,
489 the allometry of genome size and cell size (Figure 1) and the effects of genome size on
490 maximum metabolic rate (Figure 3) presented here suggest that this assumption is violated
491 in plants, as well. Modifications to the original model that relax some of its assumptions
492 have improved model predictions for plants, particularly by allowing for variation in the
493 packing of xylem conduits (Savage et al. 2010). However, the nucleotypic effects of genome
494 size have yet to be incorporated, although they may further improve models and help to
495 clarify the constraints and major innovations driving botanical form, function, and
496 diversity.

497

498 Table 1. Brief summary of traits shown previously to correlate with genome size.

499

Sizes	Reference
Pollen volume	Bennett 1972
Cell mass	Martin 1966
Epidermal cell size	Beaulieu et al. 2008; Knight and Beaulieu 2008
Nuclear volume	Van't Hof and Sparrow 1963; Baetcke et al. 1967
Nuclear dry mass	Bennett et al. 1983; White and Rees 1987
Seed mass	Grotkopp et al. 2004; Knight and Beaulieu 2008
Xylem vessel diameter	Maherali et al. 2009; Hao et al. 2013; De Baerdemaeker et al. 2018
Rates	
Cell division rate, meiosis, mitosis	Van't Hof and Sparrow 1963; Hof 1965; Bennett 1971
Minimum generation time	Bennett 1972
Leaf expansion rate	Grime et al. 1985
Phenology	Grime and Mowforth 1982
Frost tolerance	MacGillivray and Grime 1995

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504 ## Figure legends

505 Figure 1. Genome size determines the minimum size of cells, and smaller genomes enable
506 greater variation in final cell size. Data for meristematic cells (blue triangles) were taken
507 from Šímová and Herben (2012), and the solid black line is the standard major axis
508 regression through these points. Data for mature stomatal guard cells (circles and squares)
509 for ferns (dark green), gymnosperms (pink), and angiosperms (light blue) were taken from
510 Simonin and Roddy (2018), and data for mosses and hornworts (light green) were taken
511 from Field et al. (2015) and Renzaglia et al. (2017). The two regression lines through
512 mature guard cell data represent quantile regressions through the 10th (lower) and 90th
513 (upper) quantiles of the data.

514 Figure 2. Variation in the sizes and packing densities of stomatal guard cells and leaf veins
515 with variation in genome size among *Rhododendron* sect. *Schistanthe* species. The dashed
516 lines represent regressions through the 90th (upper) and 10th (lower) quantiles. Genome
517 size limits the lower limit of cell size and the upper limit of cell packing densities, and there
518 is greater variation in anatomical traits among species with smaller genomes.

519 Figure 3. Genome size limits the maximum rate of photosynthesis across C3 terrestrial
520 plants. (a) Untransformed relationship and (b) log-transformed relationship. Dashed black
521 lines are regressions through the upper 90th quantile. The solid black line is the standard
522 major axis regression ($R^2 = 0.23$, $P < 0.0001$), and the solid red line is the phylogenetically
523 corrected RMA regression.

524 Figure 4. Genome size limits the maximum rate of stomatal response (i.e. how fast stomata
525 can open or close). Data taken from McAusland et al. (2016) and Kew Plant DNA C-values
526 Database.

527 Figure 5. Relationship between genome size and ploidy for angiosperms. Each line
528 represents the SMA regression within a genus. At narrow taxonomic scales, ploidy and
529 genome size are correlated, but at broad taxonomic scales (i.e. among all angiosperms),
530 there is no relationship between genome size and ploidy due to rediploidization.

531 Figure 6. Distributions of genome size for C3 and CAM species show CAM lineages have
532 significantly larger genomes than C3 lineages. Lineages identified as CAM likely include
533 many C3 species; see text for details on identification of photosynthetic pathways.

534

535

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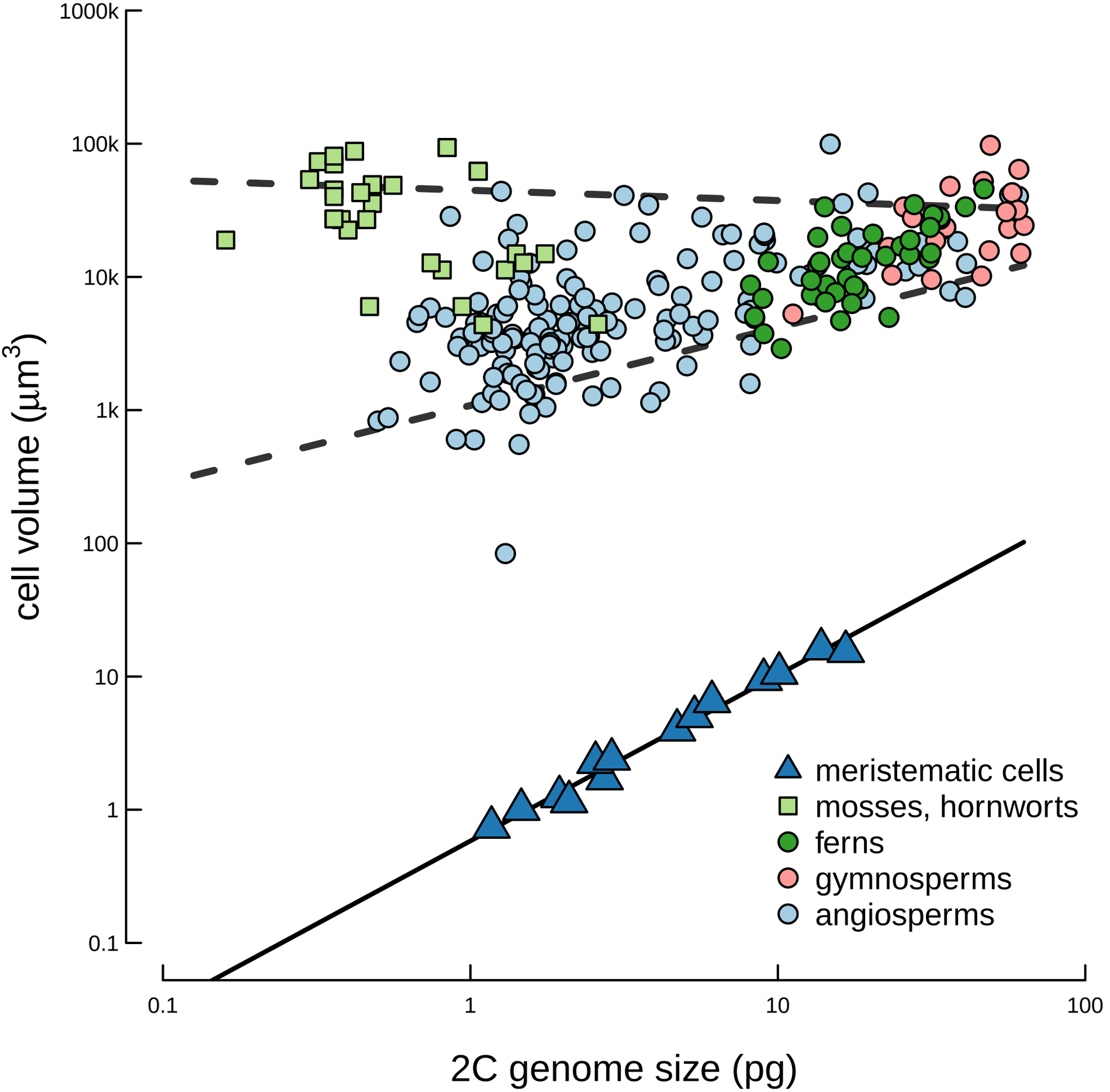
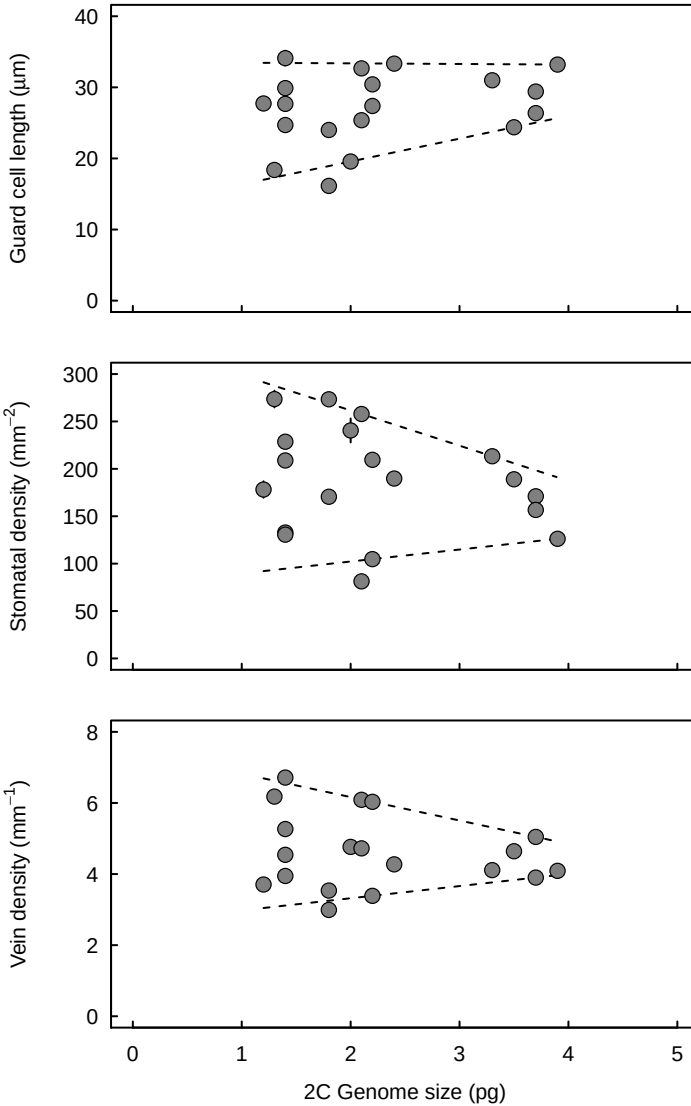
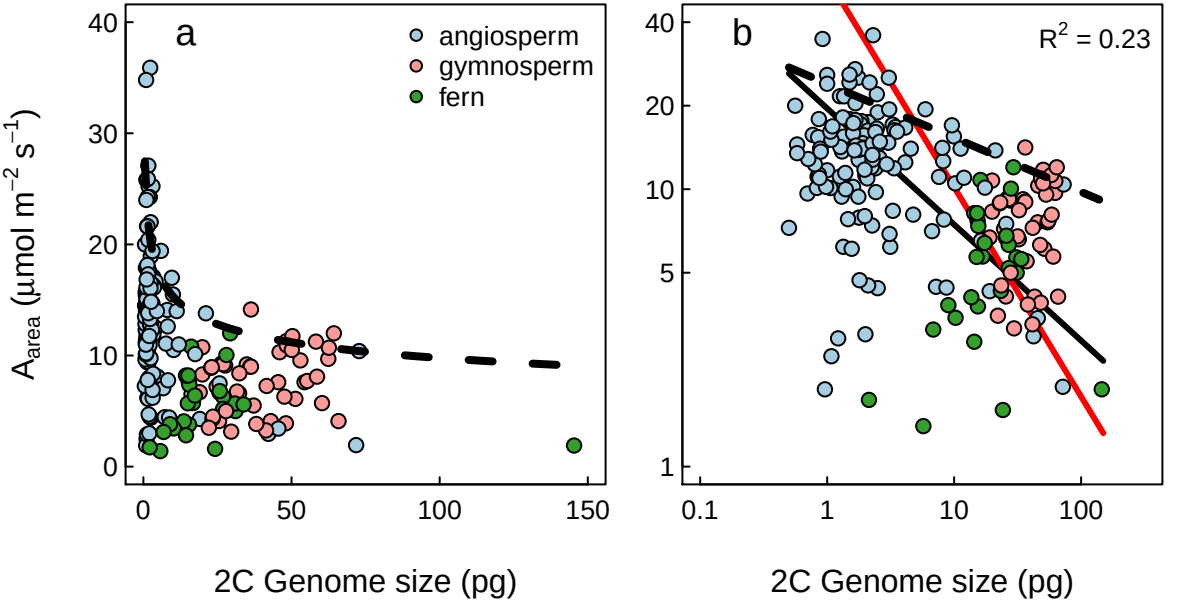
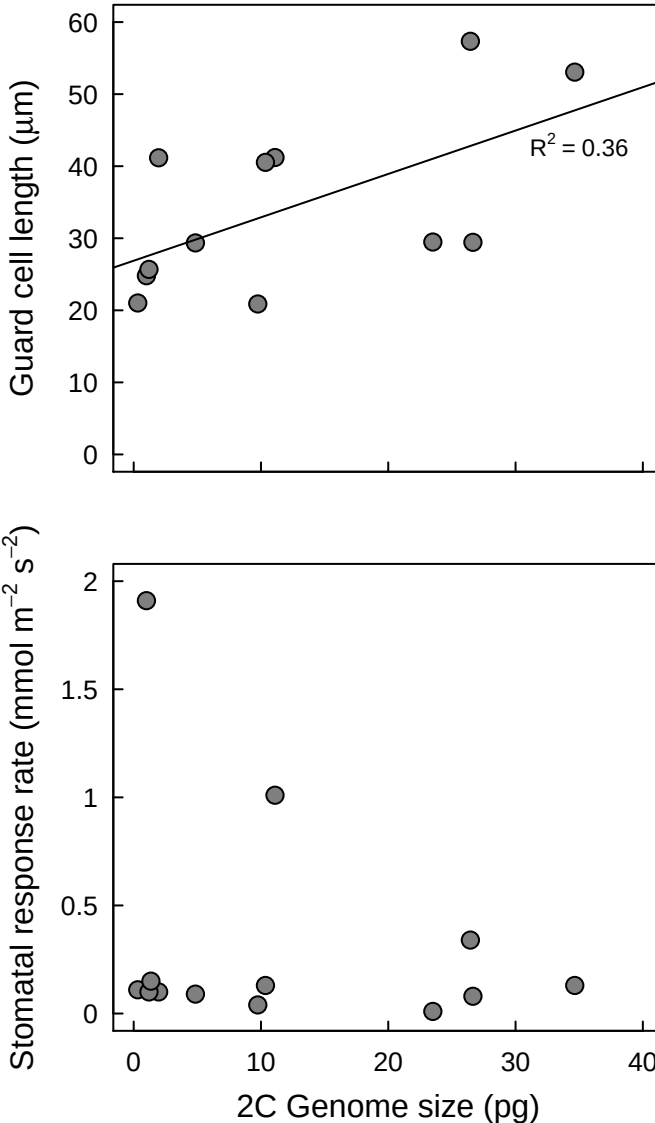
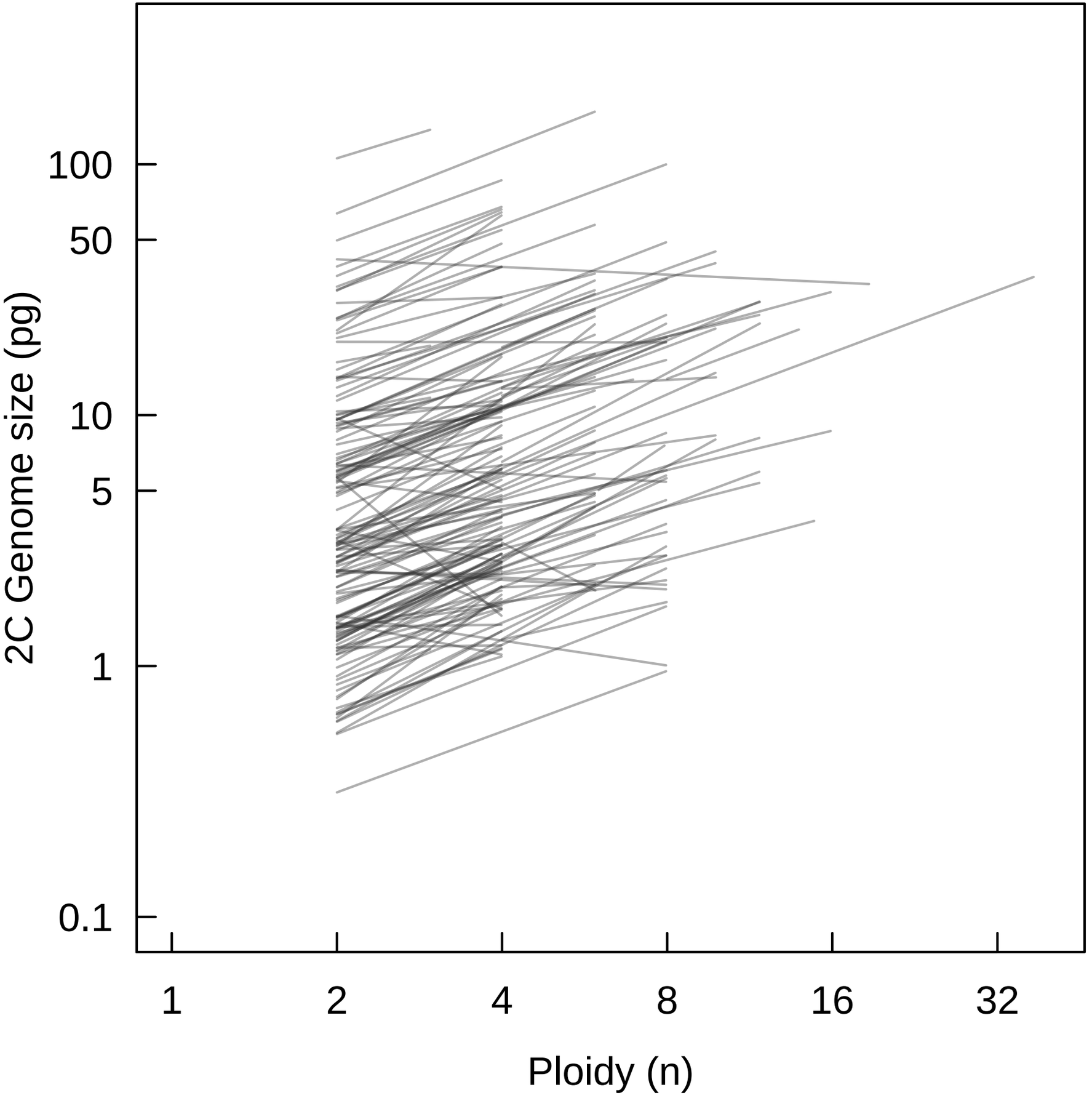
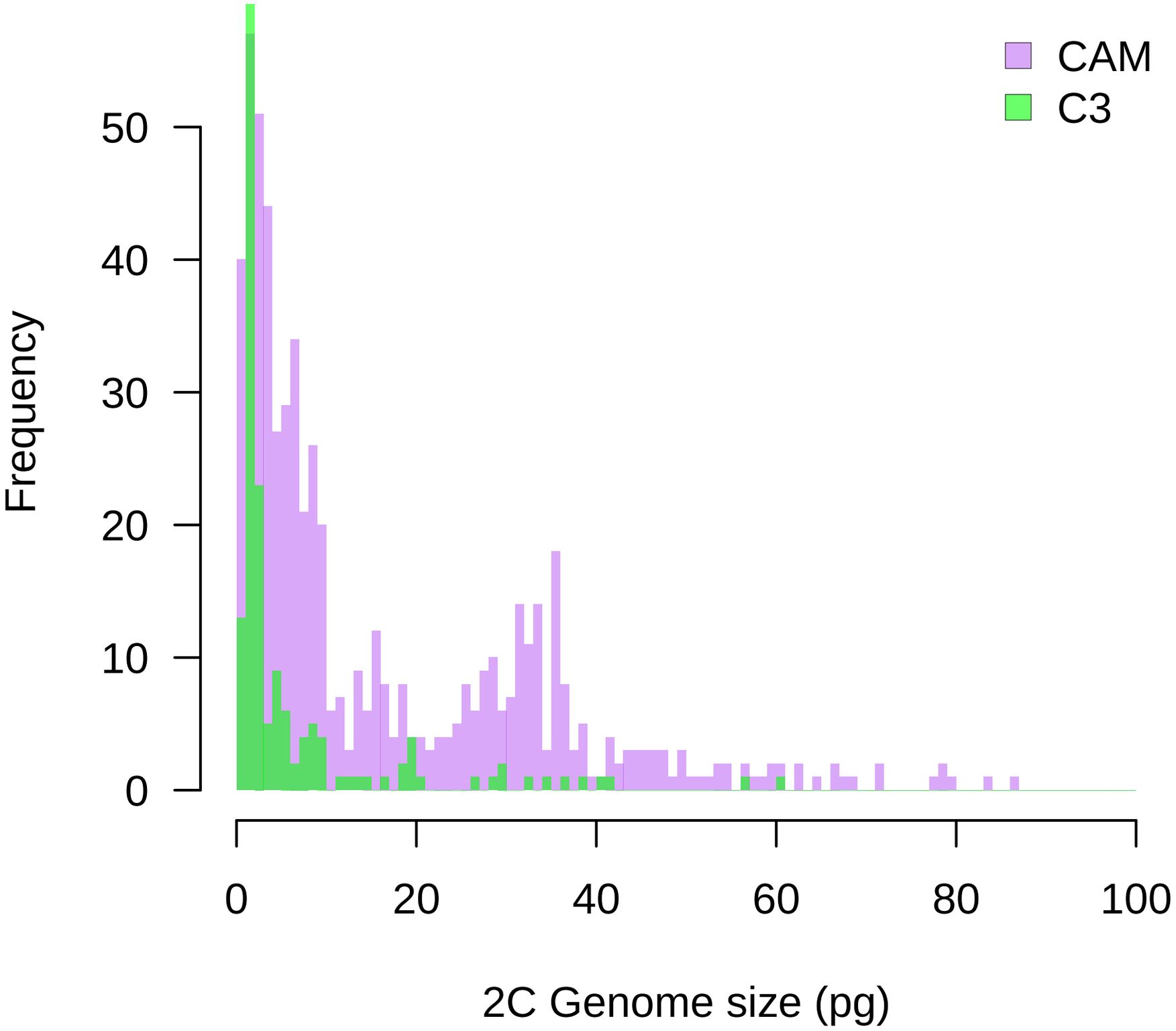

1000k
100k
10k
1k
100
10
1
0.1
cell volume (µm3)
0.1
1
10
100
2C genome size (pg)
meristematic cells
mosses, hornworts
ferns
gymnosperms
angiosperms


Guard cell length (µm)
40
30
20
10
0
Stomatal density (mm^{-2})
300
250
200
150
100
50
0
Vein density (mm^{-1})
8
6
4
2
0
0
1
2
3
4
5
2C Genome size (pg)


a
angiosperm
gymnosperm
fern
A_{area} (µmol m^{-2} s^{-1})
40
30
20
10
0
0
50
100
150
2C Genome size (pg)
b
R^2 = 0.23
40
20
10
5
1
0.1
1
10
100
2C Genome size (pg)


Guard cell length (µm)
60
50
40
30
20
10
0
R2 = 0.36
Stomatal response rate (mmol m−2 s−2)
2
1.5
1
0.5
0
0
10
20
30
40
2C Genome size (pg)


100
50
10
5
1
0.1
2C Genome size (pg)
1
2
4
8
16
32
Ploidy (n)


CAM
C3
Frequency
0
10
20
30
40
50
0
20
40
60
80
100
2C Genome size (pg)