Review

Plasticity in ploidy: a generalized response to stress

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Endoreduplication, the replication of the genome without mitosis, leads to an increase in the cellular ploidy of an organism over its lifetime, a condition termed 'endopolyploidy'. Endopolyploidy is thought to play significant roles in physiology and development through cellular, metabolic, and genetic effects. While the occurrence of endopolyploidy has been observed widely across taxa, studies have only recently begun to characterize and manipulate endopolyploidy with a focus on its ecological and evolutionary importance. No compilation of these examples implicating endoreduplication as a generalized response to stress has thus far been made, despite the growing evidence supporting this notion. We review here the recent literature of stress-induced endopolyploidy and suggest that plants employ endoreduplication as an adaptive, plastic response to mitigate the effects of stress.

The prevalence and patterns of endopolyploidy in plants

Endoreduplication is the replication of the genome without mitosis such that the nuclear DNA content (i.e., the ploidy) of the cell increases with each successive replication (generating 'endopolyploidy,' i.e., heightened ploidy within an organism; see Glossary). Although similarities exist, endopolyploidy is distinct from polyploidy in many important ways (Box 1). Endopolyploidy is common among eukaryotes, and particularly among plants, where approximately 90% of herbaceous angiosperms exhibit endopolyploidy in the majority of their tissues [1,2]. It is relatively rare among non-flowering plants, however, occurring only in the gymnosperm *Ginkgo biloba* (ginkgo) and widely among mosses (Figure 1) [3]. The occurrence of endopolyploidy in these relatively disparate groups perhaps indicates multiple evolutionary origins in land plants [4,5].

A vast mosaic of ploidy levels may be observed within an endopolyploid organism, particularly among different cell types [6–9]. For example, the highest level of endopolyploidy observed in plants is 24 576C (i.e., 24 576-fold the basic genome complement) in the endosperm of *Arum maculatum* (arum lily), although a range of 4C to 64C is typical in plants [9,10]. Very high ploidy levels (often 512C or greater) are a general feature of endosperm and suspensor cells of seed across endopolyploid taxa [9]. Very low (or the complete lack of) endopolyploidy across taxa is observed in a few cell types, including phloem companion cells and stomatal guard cells, both of which serve highly specialized functions that would possibly be disrupted by increased ploidy [7,9]. Because endoreduplication is a somatic process, the embryo and meristematic cells (e.g., procambium, root and shoot apical meristems) also lack endopolyploidy [6,7,9]. Finally, mixed ploidy among adjacent cells of the same type also occurs (e.g., leaf epidermal pavement cells range from 2C to 64C) [7,9].

Although generalized patterns of endopolyploidy may be observed within and among plants, recent evidence suggests that many plants that endoreduplicate can plastically increase their endopolyploidy beyond their 'normal' level in response to environmental factors. Given the sessile nature of plants, endoreduplication appears to be a

Glossary

C-value: the amount of DNA contained within a haplophasic nucleus (e.g., a gamete), typically measured by the number of basepairs or by mass; for a diploid organism the C-value is equivalent to genome size.
Cytokinesis: cell division, the final stage of mitosis.
Endocycle: the succession of genome replications in which the replicated genome copies remain in the same cell by omission or abortion of mitosis.
Endomitosis: the process by which mitosis is initiated but aborted before completion, where sister chromatids and chromosome segregation may or may not have occurred; can result in polyteny, doubling of nuclear chromosome number, or polynucleation depending on the timing of abortion.
Endopolyploidy: the condition in which the number of cellular genome copies has been increased through endoreduplication.
Endoreduplication: the process of complete genome replication without subsequent cytokinesis.
Genome: the complete set of chromosomes in which each is present in only one copy.
Genome size: the amount of DNA that composes a single genome copy (e.g., within a monoploid nucleus), typically measured by the number of basepairs or by mass.
Mitosis: the process of chromosome segregation and cytokinesis that results in the production of two cells with half the number of genome copies versus the initial progenitor cell.
Ploidy: an expression reflecting the number of copies of the basic genome (e.g., diploidy denotes two copies of the basic genome).
Polynucleation: the process by which mitosis is terminated after chromosome segregation, but before cytokinesis, such that multiple nuclei reform within a single cell; may also occur via cell fusion without nuclear fusion.
Polyteny: the condition of a chromosome that has been replicated but in which sister chromatid cohesion is maintained.
***n*-value:** the number of chromosomes within a haplophasic nucleus (e.g., a gamete).
Nucleotype: non-genic characters of the genome that affect phenotype.
Sister chromatids: replicated chromosomal strands that separate during mitosis to become individual chromosomes.

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valuable and commonly employed, but poorly assessed, strategy that affords plants a means of cellular optimization to local conditions that can improve their survival and fitness [1,11].

Box 1. Polyploidy versus endopolyploidy

Polyploidy is the condition of having multiple (>2) copies of the basic genome. Polyploidy is very common in plants, with evidence of ancestral polyploidy in nearly every angiosperm and fern lineage, and in approximately 60% of moss lineages [28,106,107]. Autopolyploidy results from the doubling of the basic genome by fertilization of unreduced ($2n$) gametes or from spontaneous genome doubling of a $2n$ zygote shortly after fertilization [107,108]. Allopolyploidy results from hybridization of two species, often via fusion of unreduced gametes of each species or spontaneous genome doubling of the hybrid zygote [107,108]. Regardless, the polyploid state is generally either stabilized and perpetuated, or is lost through genome downsizing and rediploidization [106–108]. Because both polyploidy and endopolyploidy entail an increase in the number of nuclear genome copies, both may be expected to impact on nucleus volume, cell volume, and other cellular properties in similar ways [108].

Polyploidy and endopolyploidy differ in many important ways, however. While polyploid and endopolyploid cells are both bound by the allelic variation they inherited, allelic diversity can be much higher in polyploid cells. For example, a cell in a tetraploid individual could contain up to four alleles at any given locus in the genome. A polyploid individual can thus harbor tremendous allelic diversity, and the new epistatic interactions between the alleles is one of the bases for the hybrid vigor often observed shortly after polyploidy is generated [106]. A tetraploid cell generated via endoreduplication from the diploid state, by contrast, would still contain at most two alleles at any locus. The effects of increased ploidy are therefore due solely to the amount of DNA present rather than to new sequence variation, although these nucleotypic effects can be plastically induced as needed by the cell, organ, or organism. Note, however, that some polyploid species also generate endopolyploidy – for example, *Beta vulgaris* (sugar beet) [109].

While polyploidy is inherited through the germline and perpetuated throughout the soma, endopolyploidy is produced by individual somatic cells. The effects of endopolyploidy on cell size, gene expression, and cell metabolism are thus not perpetuated sexually nor shared among cells. Finally, because endopolyploidy is largely generated in differentiated somatic cells, polyteny, sister chromatid separation, or polynucleation can result after genome replication. By contrast, polyploidy necessitates sister chromatid separation for mitotic and meiotic cell division. The effects, if any, of these chromosome structural differences on genome function are not well understood, however.

To date, no reviews have described the significance of plant endoreduplication in response to environmental stress. We draw here upon studies across disciplines, including horticulture, agronomy, ecology, evolution, and molecular biology, to review evidence that endoreduplication is employed as a plastic response by numerous plant taxa to help them mitigate the effects of environmental stress or otherwise fine-tune themselves to their local conditions. Specifically, we present the following: (i) an outline of the mechanistic basis of endoreduplication, (ii) the demonstrated roles of endopolyploidy in plant growth and development, and (iii) a broad purview of the induction of endoreduplication by environmental factors in plants. Finally, we present a synthesis of the evidence that endoreduplication is integrated into the generalized stress response of plants and is induced to mitigate the effects of a wide variety of environmental stresses.

The generation of endopolyploidy

Endoreduplication occurs via the endocycle, an alternative to the mitotic cell cycle that omits cell division but continues genome replication [12]. The induction and duration of the endocycle are developmentally regulated and environmentally influenced through an orchestrated suite of genetic and hormonal regulators (Figure I in Box 2), namely a variety of cyclins and cyclin-dependent kinases (CDKs) [12,13].

There are many variations of the endocycle, depending on the extent of mitotic progression and the nature of replication. If mitosis is completely omitted, the replicated sister chromatids remain cohesed as polytene chromosomes ([14], but see [15]). Endomitosis, by contrast, refers to the initiation but subsequent abortion of mitosis before cytokinesis [16]. Depending on the point at which mitosis is aborted, polyteny, sister chromatid separation, or even polynucleation may result [16]. Over- and under-replication of particular genomic regions can also occur, and is typically limited to regions with high gene expression or heterochromatin, respectively [14,17]. Although rare, the replication of individual chromosomes has also been observed (e.g., *Pinus sylvestris*, Scots pine, in water-logged, hypoxic conditions) [18].

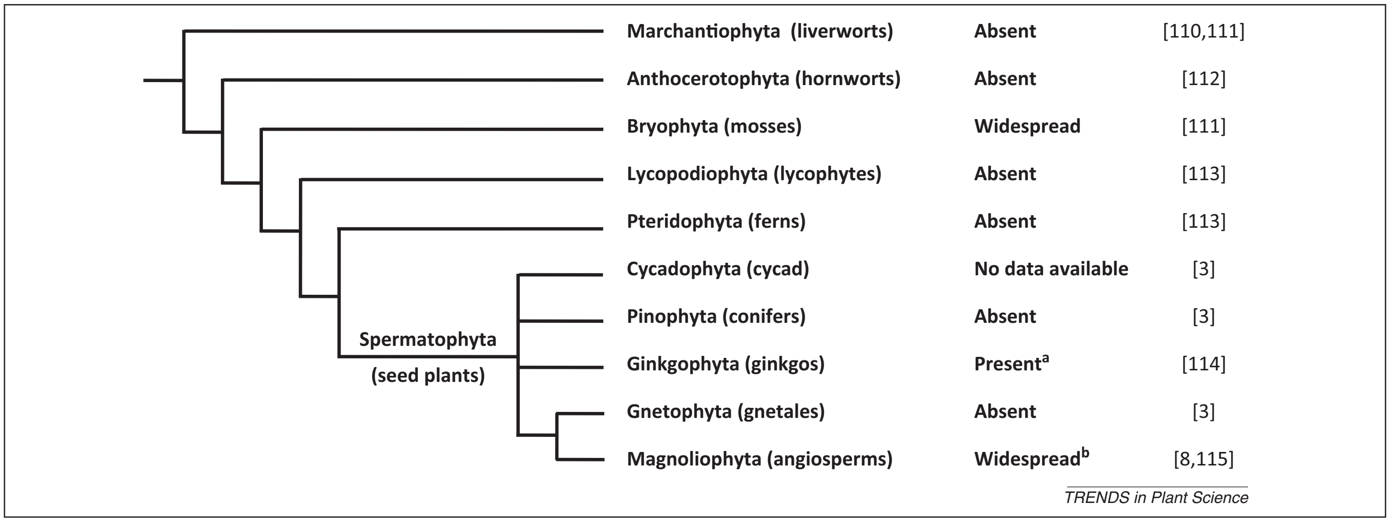

Figure 1. Occurrence of endopolyploidy in plants. Shown are extant divisions within the subkingdom Embryophyta (land plants), modified from the Tree of Life Web Project (http://www.tolweb.org). Branch lengths are arbitrary and are not correlated with divergence times [3,8,110–115]. ^{a}Endopolyploidy is present in the only extant ginkgo, *Ginkgo biloba*. ^{b}Note that many families within Magnoliophyta do not have endopolyploidy.