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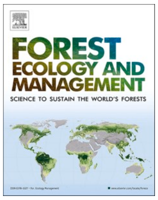

Polyploidy – A tool in adapting trees to future climate changes? A review of polyploidy in trees

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SUMMARY

Polyploidy, or genome doubling, has occurred repeatedly through plant evolution. While polyploid plants are used extensively in agriculture and horticulture, they have so far found limited use in forestry. Here we review the potentials of polyploid trees under climate change, and investigate if there is support for increased use. We find that polyploid trees like other plants have consistent increases in cell sizes compared to diploids, and that leaf-area based rates of photosynthesis tend to increase with increasing levels of ploidy. While no particular trend could be discerned in terms of biomass between trees of different ploidy levels, physiology is affected by polyploidization and several studies point towards a high potential for polyploid trees to adapt to drought stress. The ploidy level of most tree species is unknown, and analysis of geographical patterns in frequencies of polyploid trees are inconclusive. Artificial polyploid trees are often created by colchicine and in a few cases these have been successfully applied in forestry, but the effects of induced polyploidization in many economically important tree species remains untested. Polyploids would also be increasingly useful in tree breeding programs, to create synthetic hybrids or sterile triploids that could control unwanted spreading of germplasm in nature. In conclusion, this review suggests that polyploid trees may be superior under climate change in some cases, but that the potential of polyploids is not yet fully known and should be evaluated on a case-to-case basis for different tree species.

1. Introduction

Forest ecosystems contribute significantly to the diversity and production of the Earth's biomass (Bar-On et al., 2018). While there is concern for the future health of forests due to climate change (e.g., Hartmann et al. 2022), reforestation could have a significant impact by regaining control of the terrestrial carbon cycle, and help counteract the effects of climate change. A simple but so far unexplored method to enhance the robustness and productivity of many forest tree species could be polyploidy, or genome duplications. Since the 1930's, natural

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polyploids, induced mutations and polyploidization by chemicals and irradiation have been used for general plant improvement (Darrow, 1950; Sigurbjornsson and Lachance, 1987), shaping agriculture and leading farmers into the 'Green revolution' (Hedden, 2003; Jung and Till, 2021). Although many examples of polyploidization in agriculture and horticulture have led to significant improvement in productivity and trait performance (Motosugi et al., 2002, Wu et al., 2012), its application in forestry has been limited. However, there are many potential advantages of utilizing polyploids in forestry including increased resistance to abiotic stresses (e.g., Maherali et al., 2009; Tossi et al., 2022), superior performance under elevated CO_2, and changed wood properties (da Silva Souza et al., 2021).

Polyploids often have altered plant development compared to their diploid relatives. Key phenotypic differences, such as larger cell sizes for higher ploidy levels, tend to hold in ploidal series across plant orders including bryophyte, fern, gymnosperm and angiosperm lineages (Henry et al., 2014; Scholes and Paige, 2015; Alix et al., 2017; Karlin and Smouse, 2017; Šmarda et al., 2018; Wilson et al., 2021; Patel et al., 2021). Trees, however, differ from non-woody plants in having secondary growth and extended xylem. This makes trees tall and wide, giving them an edge in ecosystems when competing for light. In addition, trees have longer generation times and life spans than herbs and forbs, which may affect their potential for adaptation to rapid environmental change. Given the hypothesized evolutionary advantage of polyploids during previous environmental upheavals (Van de Peer et al., 2017), polyploids may have an adaptive advantage in their response to the challenges of climate change (Lomax et al., 2014; Faizullah et al., 2021; Ebadi et al., 2023).

There is extensive research on the evolutionary role of polyploidization and whole genome duplications (WGD) in key terrestrial plant radiation events, particularly for tracheophytes (Soltis et al., 2015; Clark and Donoghue, 2018). Even as this review was concluding, Bureš et al., (2024) explored the relationships between bioclimatic environment, genome size, polyploidy and growth form in angiosperms, and concluded that woody angiosperms were less frequently polyploid and that genome size regulation may operate differently. There is, however,

Box 1
Glossary/list of terms.

Accessory or cloud genes: Genes that are found in some, but not all, species or individuals in a taxon or taxonomic group. These genes are seen as non-essential, however, they bring uniqueness and are often advantageous to the bearer (e.g. disease resistance genes, stress tolerance, flowering time).

Allele-dosage/gene-dosage: The variable amount of gene product that is the result of multiple copies of an allele, or gene, on homologous and homeologous chromosomes.

Allopolyploid: A polyploid formed from the merging of gametes from different species or highly diverged populations.

Aneuploidy: State of organisms and cells with an unbalanced set of chromosomes with respect to their parents. Aneuploid organisms may have chromosomal instability (chromosome breakage causing gene loss) or have an abnormal number of chromosomes, such as one extra or one fewer chromosomes than expected.

Apomixis: Is the process of clonal reproduction via asexual seeds, and is often found associated with natural polyploids and ploidal variation. While apomixis often has complex evolutionary origins, and often low frequency amongst plants, the molecular basis for naturally occurring and synthetic modes of apomixis is now well understood, and may provide significant benefits to agriculture or forestry due to the fixation of hybrid vigor.

Autopolyploid: A polyploid formed by whole genome duplication (WGD) often caused by merging of unreduced gametes from individuals of the same species.

Copy number variation: The variation in the number of genes for discrete loci caused by tandem duplication, or from the number of gene loci occurring in polyploids.

Core genes: Set of genes that are shared by all individuals or species in a taxon or taxonomic group.

Diploid: Cells of an organism that have two complete sets of chromosomes, one set from each parent. Chromosomes are represented as homologous pairs in diploid organisms, and the diploid state is typical of somatic cells.

Genomics: The study of the structure, function, and evolution of the total genetic and/or epigenetic sequence information (the genome) of organisms.

Haploid: Cells of an organism that have one complete set of chromosomes, typically gamete cells.

Heterosis: Non-additive inheritance of phenotypic traits as observed from hybridization of two different parental lines, species or genera. Hybrid vigor is a highly sought after effect of heterosis.

Homeologous chromosomes: matching chromosomes in the genomes of different species. Previous to speciation, these were homologous chromosomes.

Homologous chromosomes: the matching chromosomes in two sets of chromosomes in diploids, or in more than two sets of chromosomes in autopolyploids.

Neo-functionalization: The development of a new function of a gene copy (co-option) following duplication.

Neopolyploid: A newly formed polyploid lineage. Neopolyploids can be further defined as neoallopolyploids and neoautopolyploids.

Polyploid: Cells of an organism that have more than two complete sets of chromosomes. Depending on the number of chromosome sets, they are referred to as triploid (three sets), tetraploid (four sets), pentaploid (five sets) etc.

Sub-functionalization: Gene copy expression patterns associated with different or novel time or tissue types following gene duplication.

Sub-genome: The set of chromosomes derived from distinct progenitor species.

a continued lack of understanding of the specific role of polyploidy for forest tree species during evolution. This review therefore examines if the benefits of altered plant development that are often seen in polyploid crop plants, also hold for polyploid forest trees. We summarize the contemporary research on natural and artificial polyploid forest trees to investigate whether there is evidence for the superior performance of polyploid trees under climate change conditions, and if polyploidy can be used as a tool in forestry and breeding programs to enhance the resilience of our forests.

2. Formation of polyploids and molecular effects of polyploidization

Polyploidization is an integral part of plant evolution, and most, if not all, plant genomes have undergone polyploidization at some stage (Van de Peer et al., 2017; Simonin and Roddy, 2018). While whole genome duplications within a species, autopolyploidization, can happen, allopolyploids are thought to be more common. Allopolyploids are established from hybridization between divergent lineages followed by genome duplications (Box 1, Fig. 1; Otto and Whitton, 2000; Mallet, 2007). Early research on (allo)polyploids provoked a hypothesis on a "Genomic shock" (McClintock, 1984) in the neo-(allo)polyploid species, possibly driven by transposable elements, with extensive genome-wide changes. In contrast, recent research has found a peaceful coexistence of the sub-genomes, with the regulation of different processes divided between them (e.g., Bird et al., 2018; Duan et al., 2023). Over time polyploid genomes tend to become re-diploidized (Ramsey & Schemske, 2002; Conant et al., 2014). Following the initial polyploidization event, the novel lineage undergoes genome fragmentation (Zhu et al., 2019), either with equal gene loss in both sub-genomes (Liang and Schnable, 2018), or with one sub-genome losing genes at a more rapid rate while the other becomes dominant, as in *Gossypium* (Chen et al., 2020; Conover and Wendel, 2022). This process can also result in novel genetic variation in the form of neofunctionalization or sub-functionalization, where multiple gene copies provide the opportunity for further specialization (Liang and Schnable, 2018; Van de Peer et al., 2021). Past ancestral history of polyploidization may also have a persistent influence on gene expression and genomic dominance (Yoo et al., 2013; Liang and Schnable, 2018).

While the molecular and genomic effects of polyploidization are well studied in particular crop plants, little data has so far been obtained for tree species due to their long generation times and thus difficulties in multi-generational studies. The molecular effect of hybridization, and allopolyploidization, depends on the genetic similarities between the diploid progenitors, their divergence time and differences in their gene regulation, with perhaps the most extensive effects (i.e. genomic shock) resulting from more diverged progenitors. For example, while the sub-genomes of allopolyploids have a conserved order (synteny) for the majority of their core genes, each sub-genome can also contain a unique set of genes (accessory or cloud genes) that may confer stress or disease resistance to newly formed polyploids (neo-polyploids) (Chen et al., 2020). Neo-polyploids, in particular neo-allopolyploids, may thus have important advantages over their diploid progenitors. Hybrids and neo-allopolyploids may also display heterosis and thus outperform their parental lineages. The genomic underpinnings of heterosis, however, are not very well understood, but are suggested to be controlled by a complex set of molecular processes including sub-genome dominance (Carlson et al., 2022; Carlson and Smart, 2022; Yu et al., 2021) and haplotypic divergence, changes in allele-dosage and novel regulatory interactions affecting gene expression networks (Hu et al., 2022). Examples of the latter are found in *Salix* L. (Carlson et al., 2022; Carlson and Smart, 2022), *Populus* L. (Liqin et al., 2019), and *Quercus* L. ($2n = 36$; Butorina, 1993; Dzialuk et al., 2007; Johnsson, 1946; Lefort et al., 1998; Lefort et al., 2000; Naujoks et al., 1995). The fast growth of these trees could be derived from a combination of copy number variation and heterosis.

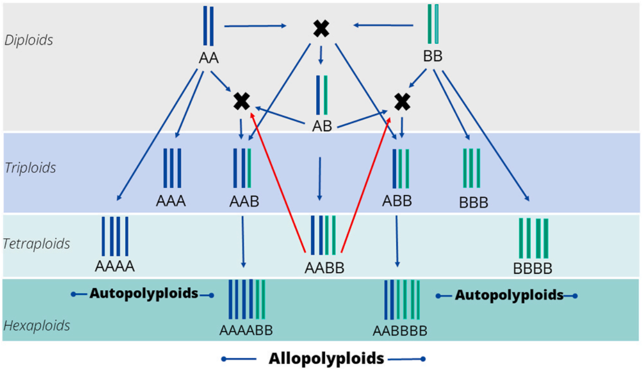

Fig. 1. Natural formation of polyploids from diploids (2x) to triploids (3x), tetraploids (4x) and hexaploids (6x). The figure illustrates autopolyploids from whole genome duplication, and allopolyploids via inter-specific hybridization and back-crossing from e.g. two different species. Modified from Yirga (2021).

3. Changes in anatomy and morphology of polyploid plants

There is a tendency across plant species that cell size correlates with genome size (Cavalier-Smith, 2005; Hodgson et al., 2010; Robinson et al., 2018), although this may be cell type dependent (Katagiri et al., 2016). Increased cell size affects a great number of key physiological processes in plants such as water holding capacity, and transport of gasses and solutes (Trojak-Goluch et al., 2021).

Since polyploid plants tend to have larger stomata that are positioned further apart compared to their diploid relatives (e.g., Šmarda et al., 2023, Fig. 2), this trait can be used to identify polyploids. This is also true for tree species across a large phylogenetic spectrum (Fig. 3a, b). Increases in stomatal cell size may be accompanied by increases in the size of other cell types, including epidermal cells and mesophyll parenchyma, resulting in thicker leaves in polyploids (Chen et al., 2021). This means that both the amount of dry mass and the water mass per leaf area may increase in polyploids compared to diploids and has been reported in several woody genera (Barceló-Anguiano et al., 2021; Li et al., 2009; Romero-Aranda et al., 1997; Zhang et al., 2019a). Larger cell sizes in polyploids do not necessarily lead to a larger surface area of leaves, as there may be a correspondingly lower number of cells in the leaves (Robinson et al., 2018). Data from woody species are contrasting, with some studies showing that polyploids have shorter, but thicker leaves than their parental diploids (Xue et al., 2017), some showing no increase in leaf area (Diallo et al., 2016; Fernando et al., 2019), and some showing larger leaf areas in polyploids (Chen et al., 2021; Hao et al., 2013; Wang et al., 2017b). The number of studies is too limited to relate these differences to phylogeny or habitats of the species.

Sizes and numbers of organelles are also affected by the level of ploidy. Larger stomata are associated with an approximate doubling of chloroplast numbers in guard cells in tetraploids compared to diploids (Beck et al., 2003; Tang et al., 2010; Shi et al., 2015; Abdolinejad and Shekafandeh, 2022), and chloroplast sizes were approximately double in tetraploid *Mangifera indica* L. compared to diploids of the same species (Barceló-Anguiano et al., 2021).

There are relatively few studies that go beyond leaf anatomy, but they seem to indicate that polyploids have larger cell sizes in other parts of the plant. For example, tetraploid *Citrus* genotypes have been shown to have thicker roots than diploids (Syvertsen et al., 2000; Ruiz et al., 2016a). Polyploids had larger structures in the hydraulic systems such as longer and wider vessel elements and sieve tube elements (Hao et al., 2013; (Barceló-Anguiano et al., 2021; De Baerdemaeker et al., 2018)). In species of *Betula* L. from China vessel diameters were larger in polyploids compared to diploids, although intervessel pits had smaller dimensions in polyploids, resulting in a larger resistance to cavitation compared to diploids (Zhang et al., 2017).

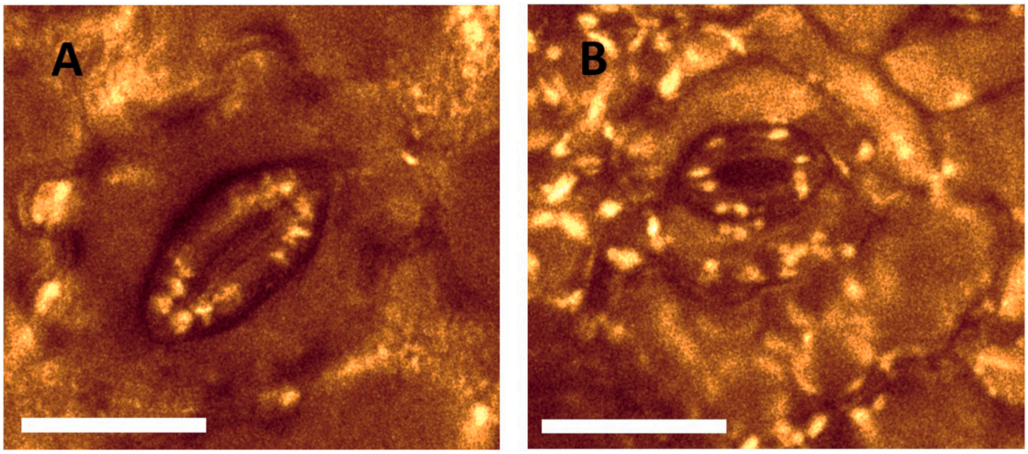

Fig. 2. The sizes of stomata are positively correlated to genome size in *Acacia senegal*. a) Tetraploid, stomata length 22.2 ± 1.4 µm. b. Diploid, stomata length 16.8 ± 1.2 µm. *n*= *10.* Bar= 20 µm.

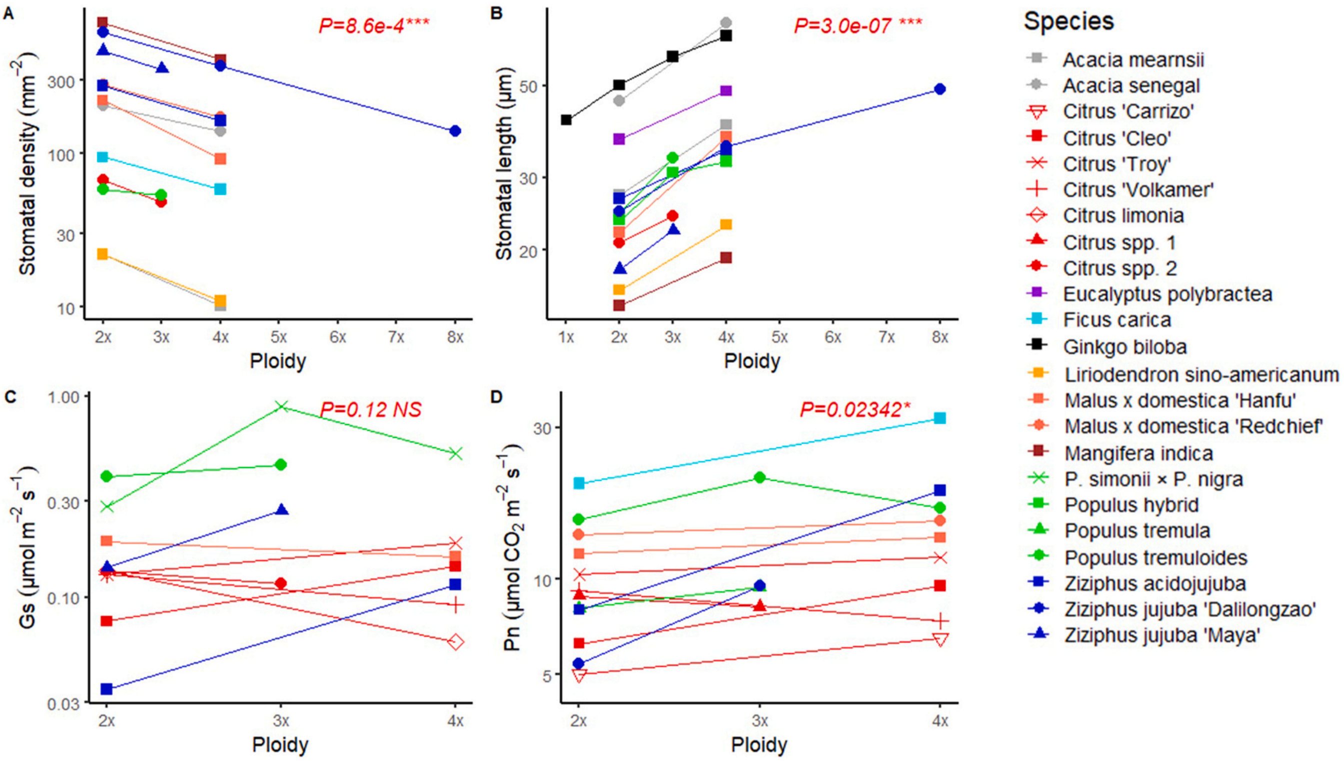

Fig. 3. Anatomical and physiological traits in tree species with varying ploidy levels. a) Stomatal density. b) Stomatal length. c) Operating stomatal conductance, Gs. d) Net photosynthesis, Pn. Inserted P-values indicate tests of effects of ploidy level from a mixed model analysis with the ploidy level as a fixed factor and species/ variety as a random factor. Data and references are available from Table S1.

Floral morphology and anatomy of trees are also affected by ploidy level, with polyploids showing overall larger morphologies than diploids (Borges et al., 2012; Fernando et al., 2019; Oliveira et al., 2022). This includes pollen (Shi et al., 2015, Mendes-Rodrigues et al., 2019) and polyads as well as stigma cups (Diallo et al., 2023). It is generally suggested that such differences could act as a reproductive barrier for gene flow between ploidy levels, thus contributing to reproductive isolation.

Although the available evidence suggests larger cell sizes throughout all organs of the polyploid plants compared to diploids, there is insufficient data to verify whether all cell types are affected to the same degree by ploidy. As a larger cell size may influence physiological performance and wood quality, there is a need for additional studies of the anatomy of polyploid trees at several levels of the plant.

4. Physiology of polyploid trees

4.1. Photosynthesis in polyploid trees

It has been hypothesized that smaller genomes are advantageous under low CO_2 conditions because this leads to smaller leaf structures and thus faster diffusion of CO_2 to the sites of photosynthetic assimilation (reviewed by Faizullah et al., 2021). This theory is corroborated by reports of extensive reduction in genome size of angiosperms during the Cretaceous, which allowed for reductions in cell sizes, higher intracellular surface areas and more efficient CO_2 diffusion into photosynthetic mesophyll cells, in turn maximizing primary productivity (Simonin and Roddy, 2018; Théroux-Rancourt et al., 2021). Polyploidization in trees may, however, have been most relevant during the Devonian and part of the Mesozoic, known for high humidity and atmospheric CO_2 concentrations (Veselý et al., 2020). Under these conditions, larger (slower) stomata would not have been detrimental to the overall CO_2:H_2O status of the plant, as they could remain open for longer periods without risking excessive water loss (Veselý et al., 2020). However, with the climatic shifts occurring during the Carboniferous to Permian periods and from the mid-Cenozoic onwards, the cooler and drier environments (characterized by low atmospheric CO_2 concentrations) may have incurred a selective pressure on stomatal downsizing to optimize intracellular CO_2:H_2O (Veselý et al., 2020; Wang et al., 2021). Yet, the only study to test this hypothesis in trees found that increases in net photosynthesis under elevated CO_2 were similar in tetraploid and diploid genotypes of the genus *Citrus* L., indicating no superiority of tetraploids in this context (Syvertsen et al., 2000).

Although very little is known about how diffusion inside the leaf is affected by changes in ploidy levels, the ploidy-induced, leaf anatomical changes may modify the diffusion pathway for CO_2 and water vapor. These leaf traits can potentially alter conductance and possibly even the CO_2:H_2O ratio. For example, larger leaves in polyploids may have greater boundary layer resistances than smaller leaves of lower cytotypes (Nobel, 1999). Stomatal conductance (g_s) in polyploids is reduced by a generally lower number of stomata per leaf area, but on the other hand could be increased by their larger pore sizes compared to diploids (Faizullah et al., 2021, Šmarda et al., 2023). Our analysis of differences in g_s among ploidy levels for a range of tree species shows no general tendencies (Fig. 3c). Thus, ploidy-induced anatomical changes to the stomatal apparatus may affect conductance and its regulation capacity. Although not directly testing for the effect of ploidy, intracellular diffusion of gasses and water have been shown to be slower in large mesophyll cells and enlarged chloroplasts compared to smaller and more densely shaped anatomies (Xiong et al., 2017; Théroux-Rancourt et al., 2021). In *Acacia senegal* (L.) Willd. and *Populus tremuloides* Michx., carbon isotopic composition suggested that water use efficiency is greater in polyploids than in diploids, as would be expected when the diffusive pathway for CO_2 is longer (Greer et al., 2018; Diatta et al., 2022).

The larger dimensions of leaves, cells and organelles in polyploids are mostly associated with increases in rates of net photosynthesis (e.g., Xue et al., 2017; García-García et al., 2020; Chen et al., 2021). A limitation of several studies is that they are based on one or two genotypes of each cytotype, restricting conclusions to the specific genotypes involved. However, our analysis across different species and genotypes indicates that photosynthesis (when expressed on a leaf area basis) is higher with increasing levels of ploidy (Fig. 3d). Still, *Populus* triploids had faster rates of photosynthesis and growth compared to diploids and tetraploids, suggesting that there is not always a direct link between genome size and physiology (Zhao et al., 2015; Zhang et al., 2019a).

There is a scarcity of studies examining the scaling effects, which come with larger genome sizes and how this interacts with plant CO_2 uptake and water loss (Wang et al., 2021). The 'large genome constraint hypothesis' was tested across phylogenies in the context of photosynthetic performance, demonstrating that photosynthetic rates (per leaf weight) were lower with increased genome size in gymnosperms, but not in angiosperms (Knight et al.,2005; Beaulieu et al., 2008). We are not aware of studies investigating this dynamic in polyploid trees. Since thick leaves may have high rates of photosynthesis (when expressed on a per-area basis) and low rates (when expressed per dry weight), a prospect lies in the possibility that methods used to estimate photosynthesis may lead to opposite conclusions regarding photosynthetic capacity in polyploid trees.

4.2. *Physiological variation of polyploid trees under drought*

There is a limited number of studies on the stress responses of polyploid trees, mainly focusing on horticultural species. However, examples of polyploid superiority (compared to diploids of the same species) include conditions of chilling stress, bacterial disease and salinity (Ruiz et al., 2016a,b; Luo et al., 2017; Zhao et al., 2017; Sivager et al., 2019, 2021; Lourkisti et al., 2020). Here we focus on climate change where drought has been identified as a major challenge.

Stress trials have shown evidence of drought resilience in polyploid trees (Diallo et al., 2016; Lourkisti et al., 2021a,b). The underlying biochemical and signaling mechanisms which cause greater drought tolerance in polyploids are not well understood. However, it has been shown that the important abscisic acid (ABA) signaling pathways are affected (Allario et al., 2013; Rao et al., 2020). In addition, osmotic adjustment and other water-saving physiological traits (in polyploid trees) could explain the apparent drought tolerance compared to diploid individuals (as is the case for *Betula* - Li et al., 1996; *Malus* - Zhang et al. 2015; de Baerdemaeker et al., 2018; *Citrus* - (Lourkisti et al., 2021a,b; Lourkisti et al., 2022; and *Mangifera indica* - Perera-Castro et al., 2023). Significantly higher concentrations of soluble sugars, proline, and glycine betaine were found in tetraploid genotypes compared with diploid genotypes of young *Ficus carica* L. (Abdolinejad and Shekafandeh, 2022). Accumulation of these compounds no doubt plays a role in plant cell-water balance.

Changed xylem anatomy in polyploids also appears to lead to changed hydraulic properties (Barceló-Anguiano et al., 2021; De Baerdemaeker et al., 2018; Hao et al., 2013). Root hydraulic conductivity of tetraploids was found to be smaller compared to diploids in both *Citrus ssp.* and *Salix viminalis* L. (Dudits et al., 2016; Ruiz et al., 2016a,b), but in other *Citrus* genotypes, the hydraulic conductivity was not affected by the level of ploidy (Syvertsen et al., 2000). In a modeling approach where polyploids were assumed to have larger vessel and sieve tube sizes, polyploids showed increased hydraulic conductance compared with diploids (Barceló-Anguiano et al., 2021). Additionally, De Baerdemaeker et al. (2018) found higher relative water content and lower stress response in autotetraploid under *in-vitro* drought conditions linked to gene expression levels for aquaporin controlling genes (MdPIP1;1 and MdTIP1;1). However, the hydraulic conductance of the shrub *Atriplex canescens* (Pursh) Nutt. decreased with increasing ploidy despite larger vessel sizes (Hao et al., 2013). This suggests that hydraulic conductance cannot be evaluated based on vessel anatomy alone. Importantly, Hao et al. (2013) found that plants with higher ploidy had smaller loss of hydraulic conductivity under tension, suggesting that polyploids would be more resistant to severe drought.

Upon water deficit conditions, vascular plants initiate systemic intercellular communication involving the phytohormones ABA and cytokinins, which eventually accumulate in the leaves and cause stomatal closure (Verslues, 2016; Takahashi et al., 2020). This reduces additional water shortages, which could occur via leaf transpiration. The ABA in tetraploid *Prunus salicina* Lindl. was found to accumulate later than in the diploid leaves under water-stress (Pustovoitova et al., 1996), attributed to the larger cells and organelles of the polyploid, thus imposing a biophysical constraint on the signaling of ABA. However, the final ABA content and cytokinin activity in the tetraploid leaves were found to exceed that in the diploid leaves. Although the transpiration rate decreased more rapidly in tetraploids under drought conditions it recovered more quickly after subsequent rehydration episodes compared to diploid plants, suggesting an acclimation response to the drought stress exhibited solely by the tetraploids after repeated drought exposure (Pustovoitova et al., 1996).

Collectively, these controlled and semi-controlled drought experiments in growth chambers and greenhouses suggest the superior performance of polyploid trees under drought. Unfortunately, this has rarely been tested in field trials. Studies under controlled conditions and in the field of diploid and triploid *Populus tremuloides* have come to opposite conclusions, pointing to an overall lower resilience to drought in triploids under field conditions (Greer et al., 2018; Blonder et al., 2021; Eisenring et al., 2023). Despite greater instantaneous water use efficiency, triploid *P. tremuloides* in the field showed lower resilience to climate-induced stress and had higher mortality than diploids (Blonder et al., 2021). Studies such as these include extraneous variables but are better indicative of the eco-physiology of polyploid trees under natural environments compared to laboratory assessments.

4.3. *Regulation of growth in polyploid trees*

The “gigantism” exhibited by the autotetraploids can be associated with altered signal transduction of indoleacetate (IAA) and upregulation of six genes involved in the biosynthesis and signal transduction of ethylene (Mu et al., 2012b). The autotetraploid *Betula platyphylla* Sukaczev has a unique phenotype compared to diploids of the same species, with a more dense stature characterized by increases in breast-height diameter, volume, leaf and catkin sizes. Also, certain triploid *Betula* lineages were found to be superior in base diameter and height to base diameter ratio when compared to the diploid lineages (Mu et al., 2012a). Both IAA and ethylene have key roles in regulating plant growth and cell enlargement, and thus their altered functions and expression in the autotetraploid could explain the altered phenotype (Mu et al., 2012b). A similar increase in biomass was reported for autotetraploids of the fast-growing deciduous species of *Paulownia elongata* S.Y.Hu (Zhi-qing, 2006). Several genes were shown to co-regulate biomass production and are thus presented as ideal targets in breeding programs (Cao et al., 2020). Amongst others, genes involved in improved chloroplast formation, and thus improved photoassimilation, were put forward to be most likely responsible for the increased biomass in the tetraploid (Cao et al., 2020).

There are, however, contrasting results between studies and species concerning the regulation of growth. Some researchers suggest that plant growth is reduced with increasing ploidy level due to increased numbers of chromosomes, which may lead to slow mitotic division, and lower overall growth (Ramsey and Schemske, 2002). In particular, meiotic and mitotic rates have been hypothesized to be slower in polyploids (compared to diploids) due to more time needed for the

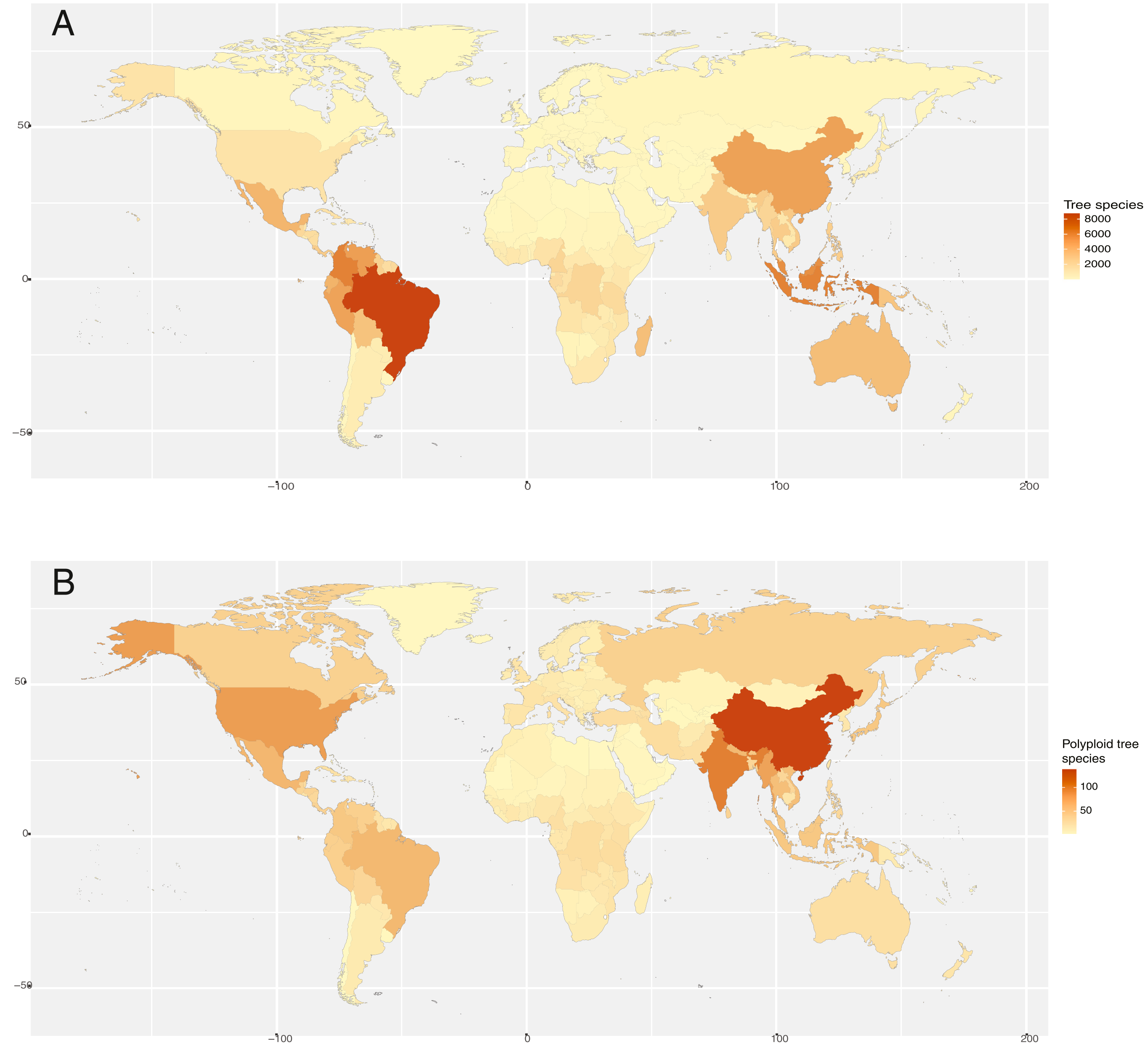

Fig. 4. a) Heat map presenting the distribution of tree species per country based on the GlobalTreeSearch database (Beech et al., 2017); b) Polyploid tree species distribution heat map generated based on the dataset from Rice et al. (2019). Note: areas with low frequencies may be under-represented in this database.

replication of the genome prior to cell division (Tate et al., 2005). Another possible explanation for slow cell division in polyploids is spatial constraints (Corneillie et al., 2019), particularly concerning the organization of chromosomes during metaphase alignment and spindle attachment, which are more likely to be perturbed or delayed due to the high number of chromosomes in the nucleus of polyploid species (Comai, 2005). Slow ontogeny has also been reported in tetraploid potato (*Solanum tuberosum* L.) (Tamayo-Ordóñez et al., 2016). However, these delays in development could be mitigated by faster and early germination by larger seeds, which is a common characteristic of polyploid plants (Tate et al., 2005; Selvi & Vivona, 2022). Growth in polyploid trees may also be limited by the increasing costs of larger cell size structures, for example pollen tube growth (Williams & Oliveira, 2020). This feature was observed in both *Betula* and *Handroanthus* species. There may also be relevant interactions between genetic background and ploidy level which may be overlooked, if single genotypes are examined. Genotype-ploidy dependent interactions have been demonstrated in *Zea mays* L., where the morphological response to ploidy change was genotype specific and shown to vary along inbred lines (Riddle et al., 2006).

Given the lack of consistency between studies, there is still a need to examine the role which genome size plays in the regulation of growth in trees. Until this is understood, the potential use of polyploid trees in forestry must be studied individually for key species and genotypes.

5. Natural occurrence of polyploidy in trees

Trees are vital for global plant biodiversity, representing about 60,000 species and nearly 20% of seed plants (Beech et al., 2017). The highest diversity of tree species is found in the tropical regions of South America, Asia, and Africa (Fig. 4a). Estimates suggest that 30–70% of angiosperms and approximately 10% of gymnosperms are polyploids (Wood et al., 2009; Rastogi and Ohri, 2020; Ohri, 2021). In general, polyploid frequency tends to increase with distance from the equator, influenced by climate, particularly temperature (Ramsey and Schemske, 1998; Rice et al., 2019; Bureš et al., 2024). In contrast, polyploid tree species appear to be more common in tropical regions (Fig. 4b). This heatmap of distribution is likely biased, however, as it is based only on a few thousand ploidy-known tree species worldwide. The exact number of polyploid tree species and the extent of natural occurrence of polyploid tree species remains unknown.

In gymnosperms, polyploids are rare and mainly found in Ephedrales and Cupressales, with high incidences in *Ephedra* L. (76%) and *Juniperus* L. (22%) (Ohri, 2021). In addition, there are stable polyploid cultivated forms of *Ginkgo biloba* L. (Šmarda et al., 2018), and the hexaploid *Sequoia sempervirens* (D.Don) Endl. is one of the most valuable timber species in the forest industry in Northern America and New Zealand (Meason et al., 2016). In angiosperms, frequencies of polyploids appear to be variable among taxonomic clades (Fig. S1, S2). At the family level, Fabaceae, Asteraceae, Malvaceae and Rosaceae have the highest numbers of polyploid woody plant genera (Fig. S1a). Forest tree genera with a relatively high proportion of polyploids, such as *Alnus* Mill., *Tilia* L., *Sorbus* L., and *Betula*, are those having their natural distribution range in the northern temperate region (Fig. S1b,c). The genus *Sorbus* (rowan) comprises some 150 species mostly in the northern temperate regions. These include mostly out-crossing diploids ($2n=2x=34$), apomictic triploids ($2n=3x=51$) and tetraploid ($2n=4x=68$) species (Hajrudinović et al., 2015; Kaplan et al., 2019; McAllister, 2005). Most of these polyploid species have deficient fertility, having originated from interspecific hybridization, and then followed by WGD in the case of tetraploidy. Therefore apomixis, which is defined as the clonal reproduction via asexual seed (Underwood and Mercier, 2022; see Box 1), provides a mechanistic advantage that allows the continued survival of triploid individuals within this genus. Since there is still relatively little genomic research on tropical tree species, the proportion of polyploids is largely unknown. This is also hampered by the immense species diversity; for example the Dipterocarpaceae, a tropical tree family that is the foundation species in many forest ecotypes in South East Asia, and is the major source of high quality hard wood in timber trade in the region, consists of around 700 species (Appanah and Turnbull, 1998).

Polyploidy can be detected by direct or indirect methods. Indirect methods rely on the analyses of morphological traits such as larger stomata in lower density and/or a higher number of chloroplasts per guard cell (see above). In contrast, direct methods measure the nuclear genome size by flow cytometry, which measures DNA content per cell, and/or chromosome counting, both of which are more accurate than indirect methods. In particular, chromosome numbers obtained visually from microscopic images provide further information, such as karyotypic variation and genome composition in polyploids, and offer deeper insights into chromosome evolution especially when using molecular cytogenetic techniques.

Estimating the number and distribution of polyploid tree species globally is challenging due to the lack of chromosome counts for most tree species. Globally, chromosome records are available for less than 20% of angiosperms and are biased toward specific clades (Rice et al., 2015). Unfortunately, only 10% of all tree species have available chromosome numbers in the Chromosome Counts Database (data retrieved 1 April 2023). Advanced techniques like estimating genome size with flow cytometry are used, but actual genome size data is available for only a fraction of plant species (Pellicer et al., 2018). To increase our knowledge, prioritizing affordable chromosome counting methods is crucial, especially in tropical and subtropical regions where tree species diversity is concentrated.

There are, however, some genera, including birch (*Betula*), that have been extensively studied. *Betula* comprises 40–60 tree/shrub species distributed from the sub-tropical and temperate to the arctic regions of the Northern Hemisphere (eFlora, 2023, Furlow, 2023). Hybridization among *Betula* species is frequent (Ashburner and McAllister, 2013; Johnsson, 1945; Walters, 1964) and hybrids are often found in the overlapping area of natural distributions. In contrast to oak (*Quercus*), beech (*Fagus* L.) and chestnut (*Castanea* Mill.) that are ploidy-stable at the genus level (mostly diploid $2n=2x=24$; Chokchaichamnankit et al., 2008; Rice et al., 2019), *Betula* is an example of a ploidy-variable genus (Fig. S2, Table S2). Among *Betula* species, the ploidy levels range from diploid ($2x$) to dodecaploids ($12x$), with the tetraploid number $2n=4x=56$ being the most common (Rice et al., 2015; Wang et al., 2016; eFlora, 2023). Overall, there are more polyploid (56%) than diploid (44%) species, and in terms of abundance and geographic range, polyploid species are more common in Eurasia than in North America (42 vs. 15 species; Table S2). Interestingly, the proportion of polyploid *Betula* species does not increase at higher latitudes as is generally observed among other flowering plants. Several arctic and alpine species are diploid, such as the dwarf birches *B. nana* L. and *B. glandulosa* Michx. (de Groot et al., 1997) and Alaskan tree birch *B. neoalaskana* Sarg. (Furlow, 2023), whereas a few sub-tropical Asiatic species are polyploid, such as *B. alnoides* Buch.-Ham. ex D.Don and *B. cylindrostachya* Wall. (both tetraploids with $2n=4x=56$, eFlora, 2023). In addition, the ratio of diploid to polyploid *Betula* species is the same in both mountain forests at high altitudes and in the lowland areas (Table S2). Thus, diploids and polyploids of *Betula* are symmetrically distributed. In the case of Alder (*Alnus* species), most polyploid species are distributed in the East Asia and Mediterranean region, whereas European and American species are predominantly diploid (Vít et al., 2017). Recently discovered tetraploid populations of *A. glutinosa* (L.) Gaertn. in Morocco (Lepais et al., 2013) and the newly described tetraploid species *A. lusitanica* Vít, Douda & Mandák and *A. rohlenae* Vít, Douda & Mandák in Southern Europe and North Africa (Vít et al., 2017) open possibilities to test the performance and potential use of these taxa in forestry.

6. Producing artificial polyploid trees for forestry

Different methods to obtain chromosome set doubling have been applied to *in vitro* cultures as a fast-track method of obtaining artificial polyploids of commercially interesting tree species like *Eucalyptus* L'Hér. (Silva et al., 2019), and also to restore fertility in newly synthesized alloploids (Sattler et al., 2016). Artificial polyploids in trees have been most frequently induced by the antimitotic agent colchicine, which mechanistically disrupts the cell cycle (Touchell et al., 2020). Different tree parts can be treated with colchicine to induce chromosome doubling, the first step in polyploidization. However, most treatments target different types of *in vitro* cultures of shoot tissues, leaf material and established meristematic tissues. Mature leaf blades of *Populus* x *hopeiensis* Hu & H.F.Chow were treated with colchicine and the induced tetraploid plants mostly came from around vein tissues (Wu et al., 2020). Furthermore, octoploid plants were derived from the tetraploid plants, and the phenotypic consequences of gene dosage effects were evaluated in the ploidy series of 2x, 4x and 8x plants (Wu et al., 2022). Allohexaploids were also generated in another effort to investigate the performance of economic traits in *Populus* with higher ploidy levels (Liu et al., 2018). In *Eucalyptus polybractea* R.T.Baker, nodal shoot cultures were successfully treated with colchicine to induce formation of thicker leaves with larger oil glands (Fernando et al., 2019). Seeds were sterilized and treated with colchicine to induce chromosome doubling in *Acacia dealbata* Link and *A. mangium* Willd. (Blakesley et al., 2002). The tetraploid plants were subsequently used for breeding to generate sterile triploid trees. Colchicine treatment of seeds was also successful for inducing tetraploids in *Platanus x acerifolia* (Aiton) Willd. (Liu et al., 2007). In horticultural tree species, like citrus and mandarin, shoot apical meristems (SAM) were treated *ex situ*, and after shoot induction grafted as scions onto trifoliate rootstocks (Aleza et al., 2009; Ollitrault et al., 2020). Such a method avoids the requirement for the introduction of material into *in vitro* culture that may pose considerable challenges for recalcitrant tree species or long-lived woody perennials.

More powerful classes of antimitotic agents, such as the herbicides dinitroanilines (trifluralin and oryzalin) and phosphoric amides (amiprophos-methyl and butamiphos; Planchais et al., 2000) are not widely used to induce chromosome set doubling in trees. Oryzalin was however used with some success to induce polyploidy in *Eucalyptus dunnii* Maiden, but the survival rate was low (Castillo et al., 2020).

7. Potential for polyploidy in forest tree breeding

The induction of polyploidy in crop species often creates opportunities and changes in breeding systems. Triploid breeding programs can be particularly beneficial, however there have been only few instances of implementation and evaluation in key forestry species, e.g., *Acacia* (Nghiem et al., 2018), *Populus* (Kang and Wei, 2022), *Eucalyptus urophylla* S.T.Blake (Yang et al., 2018) and *Betula* (Mu et al.,2012a). Naturally occurring triploids have also been identified and selected for clonal propagation due to their potential for enhanced traits and gain (*Quercus*, Dzialuk et al., 2007; *Prunus avium* L., Serres-Giardi et al., 2010; *Eucalyptus grandis* x *urophylla*, Longui et al., 2021). The low fertility of triploid oaks, likely due to disrupted meiosis and pollen production with unbalanced chromosome complements, means their direct value for downstream breeding is low (Butorina, 1993). Overall, however, it would appear that the advantages of triploid breeding in forestry programs have not yet been fully realized. In contrast, horticultural triploid breeding programs are advanced and provide significant utility. For a large variety of crops elite diploid and tetraploid parental lines are bred to produce hybrid seed, almost all of which are triploid. These progenies offer many benefits including plants with a fixed heterotic growth advantage and a uniform phenotypic distribution, along with sterility and the absence of seeds (Sattler et al., 2016). Having triploid progeny has the added advantage of containing the germplasm and avoids the release of elite breeding lines with stacked traits including disease resistance into the natural environment. Horticultural seed production is often managed using crosses onto male diploid sterile acceptor lines (Cheng et al., 2022). In this case, nuclear or male cytoplasmic sterility, or even sometimes self-incompatibility are used to manage pollination of female acceptor lines with the tetraploid pollen sources. Hybrid production in this manner usually avoids, or provides a way to tolerate endosperm imbalance which can arise from interploidy crosses during hybrid seed development (Gehring and Satyaki, 2017).

Production systems that include triploidy in forestry may require significant time for their development and assessment. Likewise, their appropriateness may need to be coordinated for forest biodiversity or the perceived risk from an invasive fertile polyploid forest tree species which may have a significant growth advantage (e.g. hybrid eucalypt species). Even so, polyploidization in forest breeding programs may provide other useful opportunities. Synthetic polyploid systems have been used to overcome breeding barriers, and perform wide hybridizations (Manzur et al., 2015; Ruiz et al., 2020), or regain fertility (Rieseberg, 2001). While fertility is often unaffected in induced autopolyploids, since endosperm balance is unchanged during seed development, synthesized allopolyploid hybrids can have reduced fertility. Often the restoration of fertility occurs through further doubling of allopolyploids, and can be attributed to a number of specific mechanisms (Rieseberg, 2001). These include modifying the ploidal balance between subgenomes, balancing the divergence between the parental subgenomes, or eliminating of specific genomic sequences, and improving the stability of the hybrid genome. In other cases, post-zygotic atrophy can occur at the F1 generation (Manzur et al., 2015), and fertile individuals are sometimes obtained by embryo rescue. Even considering those barriers, there are many examples where synthetic polyploids have acted as a bridge between species of different ploidy levels, allowing new genetic diversity, via introgressive hybridization, to be tapped into plant and tree breeding programs.

Changed ploidy levels can sometimes be associated with clonal reproduction via asexual seeds or apomixis (eg. *Sorbus*; Box 1). This is often observed at low frequency in tree species, and often unlikely to have significant impact on population structure, with the exception of *Mangifera*, *Citrus* and *Sorbus* for example, where obligate modes of apomixis can and do occur (Hamston et al., 2018; Wang et al., 2017a; Yadav et al., 2023). The molecular basis for apomixis is now well understood (Underwood and Mercier, 2022), and engineering of apomixis into different crops has been recently achieved (Vernet et al., 2022; Underwood et al., 2022). Similar to triploid breeding programs, apomixis offers the potential for the fixation of hybrid vigor, and a method to evaluate morphological plasticity and niche adaptability. Furthermore if asexual seed reproduction were ever to be introduced into key forestry species, individuals with polyploid genomes may be better suited for the expression of both parthenogenesis and modifier loci (Hojsgaard, 2018). Apomixis on the other hand, will not provide a suitable method of germplasm containment for an elite breed of forestry trees should that be necessary.

8. Uses of polyploids in forestry

The many examples of accelerated vegetative growth in polyploids (Beyaz et al., 2013, Chen et al., 2021) have led to an interest to test the potential of both natural and artificial polyploid trees for forestry purposes. While examples of polyploid trees are numerous in horticulture, the number of natural polyploid tree species that are currently in use in forestry is relatively limited. Still, the list of currently ploidy-known trees and shrubs in Table S3 contains commercially used species, including many shrub species but also important forestry species such as *Acer pseudoplatanus* L., *Fraxinus chinensis* Roxb., and several tropical timber genera such as *Shorea* Roxb. ex C.F.Gaertn. and *Cordia* L. Trees that naturally display multiple levels of ploidy are predominantly found amongst angiosperm trees and provide valuable material for testing effects of ploidy on field performance, like *Acacia senegal* (Diallo et al., 2016) and *Populus tremuloides* (Arno and Hammerly, 2020, Blonder et al., 2021). *Betula* (Table S2) contains several valuable polyploid species, including *B. chinensis* Maxim., which is one of the most valuable timber trees in northern China (eFlora, 2023), and the North American paper birch (*B. papyrifera* Marshall, comprising tetra-, penta- and hexaploids), one of the most sought after wood tree species for building and other purposes (Furlow, 2023). In northern Europe, the tetraploid *B. pubescens* Ehrh. is a common species that has previously been bred for both better timber quality and growth rate with great efficiency (Niemistö et al., 2017).

Recent studies have sought to specifically characterize the correlation between ploidy levels and lignin contents in trees as wood with lower lignin content is a desirable trait for certain applications. In *Arabidopsis*, induced tetraploid plants producing higher biomass than the diploids also had a lower lignin content (Corneillie et al., 2019). However in wild-type *Populus tremula* x *P. alba*, the tetraploid plants had lower biomass production and a higher lignin content than the diploids (Wouters et al., 2022), whereas in a synthetic poplar allotriploid induced by *Populus pseudosimonii, P. nigra 'Zheyin3#'* and *P. beijingensis* hybridization, the lignin content was reduced compared to the diploids (Xu et al., 2022). A lower lignin content in triploids was also found in *Populus x tomentosa* Carrière (Yao and Pu, 1998) and *Salix* hybrids (Serapiglia et al., 2015). The mechanism suggests a regulatory function for lignin biosynthesis associated with triploids.

In fruit trees, artificial polyploids are sometimes characterized by dwarfism (Ruiz et al., 2020). However, field trials of important forestry species, including *Acacia senegal* (Diallo et al., 2016), *Liriodendron x sino-americanum* P.C.Yieh ex C.B Shang & Z.R.Wang (Chen et al., 2021) and *Populus tremula* (Pärnik et al., 2014) show increased growth in polyploids compared to diploids. In a short term experiment, triploid hybrid *Populus* clones grew faster than diploids and tetraploids formed from the same parental origins (Zhao et al., 2015; Zhang et al., 2019b). However, there was no unidirectional response of growth upon polyploidization in *Salix viminalis* L., where clones of autotetraploids exhibited either faster or slower growth compared to the parental diploid (Dudits et al., 2016). Similar results were obtained in *Populus* hybrids where, depending on the line, polyploids generated by protoplast fusion showed both superior and inferior biomass compared to the parental lines (Hennig et al., 2015). Triploid tree species such as Chinese white poplar (*Populus x tomentosa*) and willow (*Salix* spp.) have been used as model tree species to explore growth traits. For these species, triploids had increased growth and a more desirable wood composition, which can be exploited in breeding programs aimed at optimizing biofuel production (Zhang et al., 2012; 2013; Serapiglia et al., 2015).

Other angiosperm trees with high commercial value have also been shown to develop better traits when growing as artificial polyploids. *Paulownia* Siebold & Succ. are adaptable and fast-growing deciduous trees that provide raw material for manufacturing and agroforestry, and many traits related to growth and stress resistance were found to be superior in the colchicine induced autotetraploid *Paulownia australis* (PA4) compared to the parental diploid (PA2) (Xu et al., 2015).

Globally, *Eucalyptus* is the most important angiosperm tree genus for pulp production (Myburg et al., 2014). Efforts to improve wood traits through polyploidization have shown promising results for eucalypt hybrids (*E. grandis x E. urophylla*) where the wood from synthetic polyploid clones had lower basic density and longer fibers compared to diploids (da Silva Souza et al., 2021). The two parental genomes were also shown to differ significantly in the repertoire of duplicated genes and for structural variation (Shen et al., 2023), highlighting how allopolyploidization can benefit forestry related trait breeding through the combination of significant genome diversity. Artificially induced polyploids have also been obtained for *E. dunnii* as part of the breeding program to obtain new genotypes with improved adaptability and possibly reduced flowering age (Castillo et al., 2020). However, in another study of *E. grandis x E. urophylla* hybrids, polyploids exhibited decreased growth compared to their diploid counterparts (da Silva Souza et al., 2021). Similar results were obtained in a study comparing polyploid and diploid *E. polybractea* R.T.Baker grown in field and greenhouse conditions where the polyploids were shorter and thinner than the diploids (Fernando et al., 2019).

Since gymnosperm trees, in particular species within the genera *Pinus* L., *Picea* Mill. and *Larix* Mill., includes several commercially important species, efforts have been made to produce superior traits through the generation of colchicine-induced polyploids. In a 30 year-long study of polyploids from *Pinus sylvestris* L.*, Pinus contorta* Douglas, *Picea abies* (L.) H. Karst. and *Larix sibirica* Ledeb. in Sweden (Johnsson, 1975), the trees remained tetraploid but cone production did not occur until 30 years of age. The pollen formation was abnormal, preventing generation of triploids and seed quality was very poor in the C1 generation generated from backcrosses to the diploid parents. As the polyploids displayed growth delays and even dwarf growth, further efforts towards applying polyploids to these breeding programs were discouraged (Ahuja, 2005).

9. Perspectives

Forestry will play a significant role in regaining control of the terrestrial carbon cycle from the over-exploitation of fossil fuels, and polyploid trees could play an important role by accelerating biomass accumulation. For most forestry tree species, however, there is no data on the effects of increased ploidy on fitness. Increased knowledge of the potential benefits of elevated ploidy levels from either allo- or autopolyploidization would directly benefit forestry and guide future research in this area. As we have reviewed above, increased ploidy may in some cases have positive outcomes on traits like growth, biomass, timber properties and resistance to climate related stressors.

To address the knowledge gap in chromosome counts for plants, particularly trees, focused efforts in chromosome counting or flow cytometry are needed, especially in biodiversity hotspots such as Brazil, Southeast Asia, and Madagascar. Targeting selected forest tree genera for comprehensive chromosome counting and obtaining intraspecific chromosome numbers will aid in conservation efforts and help identify biodiversity (Severns & Liston, 2008).

While numerous studies indicate that polyploidy leads to larger cellular structures at the leaf surface, there is little knowledge on how the structural development inside leaves, stems and roots are affected. This also means that links between anatomy and physiology are poorly understood for polyploids. In particular, the ratio between photosynthesis and transpiration (water use efficiency) may be increased following polyploidization, but there is a large gap in data despite it being easily measurable using for example carbon isotopic discrimination. The often hypothesized superior performance of polyploids under high CO_2 environments has received surprisingly little attention by physiologists and it should be a priority to test this, especially when combined with stress trials.

Along with understanding the ecophysiological significance of polyploidy, experiments on the polyploidization of forest trees can further clarify the molecular basis for the control that genome size exerts on plant form, anatomy and physiology. Experimental polyploidization of key forest trees may also refine inferences on the paleo record especially for stomatal density/index relationships, since induced ploidal series could provide contemporaneous reference collections and extend data observations in the fossil record from the nearest living equivalents. A close monitoring of new polyploids under field conditions is necessary, not only to evaluate the performance outside laboratories and greenhouses, but also to evaluate the potential invasiveness if polyploids prove superior to conspecific diploids.

Taken together, polyploidy provides substantial potential for breeding of both horticultural and forestry trees for traits facilitating adaptation to the changing climate, yet this potential needs to be studied on a case-by-case basis in different tree species.

CRediT authorship contribution statement

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original draft. **Immanen Juha:** Writing – review & editing, Writing – original draft. **Martens Helle Jakobe:** Writing – review & editing, Writing – original draft, Visualization. **Koutouleas Athina:** Writing – review & editing, Writing – original draft, Visualization, Data curation. **Strömvik Martina:** Writing – review & editing, Writing – original draft. **Ræbild Anders:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Salojärvi Jarkko:** Writing – review & editing, Writing – original draft. **Vivian-Smith Adam:** Writing – review & editing, Writing – original draft, Visualization. **Egertsdotter Ulrika:** Writing – review & editing, Writing – original draft, Conceptualization. **Vatanparast Mohammad:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation. **Anamthawat-Jónsson Kesara:** Writing – review & editing, Writing – original draft, Formal analysis, Data curation. **Nieminen Kaisa:** Writing – review & editing, Writing – original draft. **Röper Anna-Catharina:** Writing – review & editing, Writing – original draft, Visualization. **Olofsson Jill Katharina:** Writing – review & editing, Writing – original draft, Visualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are attached as supplementary materials.

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List of supplementary materials

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.121767.:

Figure S1. Polyploid occurrence in different taxa. a) Bar chart representing the frequency of polyploid tree/shrub species per family. b) Bar chart representing the number of polyploid species for genera with the highest number of species. c) Bar chart representing the frequency of polyploid tree/shrub species per genus. Tree genera such as *Alnus*, *Tilia*, *Sorbus, Carya* and *Betula* are among the top forest trees. Our approach to classify the polyploids followed Rice et al. (2019) in which polyploids are explicitly defined as those taxa that have undergone a polyploidization event since divergence from the most recent common ancestors. The species are considered diploid when all chromosomes counting for the taxa are diploid, whereas species with at least one record of ploidy are shown as polyploid.

Figure S2. Distribution of ploidy levels of Betula species using Eye-Chrom R package (Rivero et al., 2019).

Table S1. Literature data on anatomy and physiology of polyploid trees (Excel file).

Table S2. List of 57 ploidy-known, naturally occurring Betula species, with geographical distribution, from the total of about 65 species worldwide. (Word file).

Table S3. List of currently known polyploid trees and shrubs based on the chromosome counts database (Rice et al., 2019), retrieved April 1, 2023 (Excel file).

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