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REVIEW
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Anthropogenic Impacts on Meiosis in Plants

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As the human population grows and continues to encroach on the natural environment, organisms that form part of such ecosystems are becoming increasingly exposed to exogenous anthropogenic factors capable of changing their meiotic landscape. Meiotic recombination generates much of the genetic variation in sexually reproducing species and is known to be a highly conserved pathway. Environmental stresses, such as variations in temperature, have long been known to change the pattern of recombination in both model and crop plants, but there are other factors capable of causing genome damage, infertility and meiotic abnormalities. Our agrarian expansion and our increasing usage of agrochemicals unintentionally affect plants via groundwater contamination or spray drift; our industrial developments release heavy metals into the environment; pathogens are spread by climate change and a globally mobile population; imperfect waste treatment plants are unable to remove chemical and pharmaceutical residues from sewage leading to the release of xenobiotics, all with potentially deleterious meiotic effects. In this review, we discuss the major classes of exogenous anthropogenic factors known to affect meiosis in plants, namely environmental stresses, agricultural inputs, heavy metals, pharmaceuticals and pathogens. The possible evolutionary fate of plants thrust into their new anthropogenically imposed environments are also considered.

Keywords: anthropogenic, meiosis, recombination, plants, pollution, evolution

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INTRODUCTION

Humanity's impact on natural ecosystems is well documented and has led to a decline in biodiversity globally (Cardinale et al., 2012; Hautier et al., 2015). The anthropogenic drivers responsible for this are predominantly related to climate change and pollution that stem from the agricultural and industrial demand to support an ever-growing population. These factors are also known to effect cellular processes, meiosis being particularly vulnerable. The meiotic process is key for all sexually reproducing organisms as it is responsible for halving the chromosome number during gametogenesis and for the process of recombination which generates much of the genetic diversity. The biochemical processes underpinning meiosis are highly conserved but can be influenced by both abiotic and biotic stresses (Modliszewski and Copenhaver, 2017).

Atmospheric and terrestrial pollutants, and xenobiotic compounds (defined as any non-biological compounds that have a detrimental effect on the organism) are prevalent in the environment. The actual number of such compounds is difficult to ascertain accurately, but the United States Environmental Protection Agency currently lists over 85,000 substances on their Toxic Substances Control Act Chemical Substance Inventory (Donner et al., 2010; European Psychiatric Association [EPA], 2018[1]). The genotoxicity of such compounds on plants has been assayed using a variety of methods and a range of plants species including *Tradescantia paludosa*,

[1]https://www.epa.gov/tsca-inventory

Allium cepa, and *Vicia faba* (Kristen, 1997). The assays involve exposing plants to a known pollutant and assaying the number of chromosome aberrations induced. Initially, assays utilized root cells undergoing mitosis but it was later realized that meiotic cells were far more sensitive to such compounds (Kristen, 1997). The most widely used assay is the *Tradescantia* Micronucleus-in-Tetrad Assay for Environmental Mutagenesis, commonly referred to as the Trad-MCN assay (Rodrigues et al., 1997). The Trad-MCN assay detects micronuclei formed during meiosis, and has been used for *in situ* and *in vivo* laboratory tests to determine the genotoxicity of pollutants in the air, water and soil. The sensitivity of this assay is staggering; for example, plants exposed to various brands of air fresheners for between to 1–6 h results in a significantly higher number of micronuclei (Ma and Harris, 1987a,b). Such assays emphasize the sensitivity of meiosis to external factors.

In some instances, it is desirable to alter the meiotic process, and there has been a resurgence in interest to modulate the recombination landscape in crop plants in order to increase genetic variability for selection in advanced breeding programs. The benefit to plant breeding is clear, but for non-crop plants such destabilizing factors could be detrimental and could confer selective disadvantage. The aim of this review is to examine anthropogenic factors such as climate, agrochemicals, heavy metals, combustible gasses, pharmaceuticals and pathogens, which are known to influence meiosis in a range of plant species (summarized in **Table 1**).

ENVIRONMENTAL STRESSES

It is now generally accepted that human activity is responsible for climate change (International Plant Protection Convention [IPPC], 2014), which is manifested as a rise in global temperature and carbon dioxide levels, more extreme and unpredictable weather patterns, and a rise in sea levels with its concomitant increased risk of salinisation of ground water. These changes are very likely to challenge our agricultural productivity and threaten global food security. As a consequence, it is imperative that we understand the plant's response to abiotic stresses, as this will inform our strategies of intervention to protect and adapt future crops (Mickelbart et al., 2015). This section focusses upon the effects of environmental stresses on meiosis and recombination in some model, crop and non-crop species. It is pertinent to consider this process in this context, since recombination is fundamental to the fertility, genetic stability and genetic potential of sexually reproducing organisms.

Through exhaustive investigation, we now have a very good idea of how meiosis works (Wang and Copenhaver, 2018), and how external stresses may invoke certain adaptive and ameliorative responses in plants (De Storme and Geelen, 2014; Bomblies et al., 2015; Modliszewski and Copenhaver, 2017). Suboptimal high and low growth temperatures and their effects on modulating crossover (CO) frequency and distribution in plants have received particular attention, and have long been recognized in plants. In most instances, such adjustments in CO landscape have been inferred from observing chiasmata, the cytological equivalents of COs at metaphase I. Elliott (1955) showed that there was a reduction of CO frequency in meiosis in *Endymion nonscriptus* at 20°C but not between 1 and 15°C. These observations are not consistent with a subsequent study, which showed a consistent but gradual decrease in mean chiasma frequency with increasing temperature in this species (Wilson, 1959b). This difference could be explained by genetic and environmental influences beyond temperature. Dowrick (1957) recorded an increase in interstitial chiasmata with increasing temperature in *T. bracteata* and *Uvularia perfoliata*, Elliott (1955) showed a detrimental effect on chiasma frequency at 20°C in *Hyacinthus orientalis*, and Lin (1982) showed that chiasma frequency is reduced at 37°C in *Rhoeo spathacea*. A combination of water and temperature stress in two varieties of *Hemerocallis* induces desynapsis (Karihaloo, 1986, 1994). High temperature induces meiotic irregularities and diploid pollen formation in species of *Rosa* (Pecrix et al., 2011) and *Populus* (Wang et al., 2017; Tian et al., 2018), which is considered to have important implications in terms of adaptation and evolution through polyploidisation. Recombination frequencies in *Arabidopsis thaliana* are positively correlated with temperature over the range 19–28°C (Francis et al., 2007), but this response appears to be part of a U-shaped curve in which chiasma frequencies rise from a low at 18°C to higher values at both 8 and 28°C (Lloyd et al., 2018). The changes involve class I interfering COs only (Modliszewski et al., 2018), in contrast to the observations in barley (*Hordeum vulgare*) described below.

The studies above describe temperature effects on recombination in non-crop species. Whilst these have value in forwarding our knowledge and understanding of fundamental biological processes, they cannot substitute for studying these effects in the crops themselves, especially given the variation in responses of different plants, which confounds direct translation from one species to another. Unfortunately, there is a dearth of systematic studies of this phenomenon in crop plants, but several particular crops stand out. Prakken (1943) showed that high temperature and drought together exacerbated reduced bivalent formation in asynaptic rye, and Saini et al. (1984) showed that temperature and water stress together caused male sterility in wheat, but not through any demonstrable negative effect on meiosis. The latter contrasts with more recent observations, which show that heat stress induces meiotic chromosomal abnormalities in four wheat cultivars, and various changes in meiotic defects in some cereal crops (Rezaei et al., 2010; Omidi et al., 2014). Si et al. (2015) showed that some but not all rice (*Oryza sativa*) plants subjected to heat stress had higher recombination frequencies. Powell and Nilan (1963) described by cytology significantly higher chiasma frequencies at higher temperatures in an inversion heterozygote of barley. In contrast, Jensen (1981) used genetic mapping of barley to show that temperatures of 12, 18, and 24°C had no effect on recombination frequencies. Higgins et al. (2012) later reported that a rise in temperature not only increases the CO frequency, but also redistributes COs to more distal chromosomal locations. Since COs are highly distally localized

TABLE 1 | Summary of anthropogenic factors and their influence on meiosis.

Factor	Species	Phenotype*	Reference
Temperature	*Arabidopsis thaliana*	↑CO	Francis et al., 2007
	Hordeum vulgare	↑CO	Phillips et al., 2015
	Endymion non-scriptus	↓CO	Elliott, 1955
		↓CO	Wilson, 1959b
	Hyacinthus orientalis	↑↓CO	Elliott, 1955
	Oryza sativa	↑CO	Si et al., 2015
	Populus pseudo-simonii	St, L, M, PM, Sp	Wang et al., 2017
	Rhoeo spathacea	↓CO	Lin, 1982
	Rosa spp.	Sp	Pecrix et al., 2011
	Tradescantia bracteata	↑CO	Dowrick, 1957
	Triticum aestivum	PM, L, M	Omidi et al., 2014
	Uvularia perfoliata	↑CO	Dowrick, 1957
Water stress	*Zea Mays*	↑CO	Verde, 2003
	Oryza sativa	U, L, M	Namuco and O'Toole, 1986
	Sesbania cannabina	PM, U, L	Srivastava and Kumar, 2016
	Hemerocallis	M	Karihaloo, 1986
		M	Karihaloo, 1994
Salinity	*Arabidopsis thaliana*	↑CO	Boyko et al., 2006
		↑CO	van Tol et al., 2018
Nutrient solution	*Gilia millefoliata* × *G. achilleaefolia*	↑CO, ↓B	Grant, 1953
	Solanum lycopersicum	↑CO	Griffing and Langridge, 1963
	Triticum aestivum (-Ph1)	↑CO	Martín et al., 2017
Potassium	*Lolium temulentum*	↑CO	Law, 1963
	Pennisetum glaucum	↑CO	Dhesi, 1975
Phosphate	*Secale cereale*	↑CO	Bennett and Rees, 1970
	Hordeum vulgare	↑CO	Fedak, 1973
	Pennisetum glaucum	↑CO	Dhesi, 1975
	Festuca pratensis (2x and 4x)	↓M	Deniz and Tufan, 1998
	Arabidopsis thaliana	↑↓CO	Barth et al., 2000
Nitrogen	*Secale cereale* (4x)	↑Bivalent	Hossain, 1978
Herbicide	*Hordeum vulgare*	St, B, M	Wuu and Grant, 1966
		St, B, F, M	Wuu, 1967
		↓CO	Sharma et al., 1981
	Sorghum vulgare	A, Sp	Liang et al., 1969
		A, Sp, U	Lee et al., 1974
		A, B, L	Soriano, 1984
		Multiple nucleoli, PM	Currie and Liang, 1996
	Vicia faba	St, L, B, M, A	Amer and Ali, 1974
		St	Badr et al., 1987
	Triticum durum	B, L	Razu et al., 2014
Insecticide	*Hordeum vulgare*	St, B, F, M	Wuu, 1967
	Vicia faba	St, B, L	Amer and Ali, 1968
		St, B, L	Amer and Farah, 1968
		St, B, L, Sp	Amer and Farah, 1976
		St, B, F, L, U, Sp, M	Amer and Farah, 1980
		St, L, B	Amer and Farah, 1983
		St, B, F	Amer and Farah, 1987
	Capsicum annuum	St, B, L, Sp, M	Devadas et al., 1986
		St, B, L, M, U	Reddy and Rao, 1981
		↓CO, S, B, L, U, M	Lakshmi et al., 1988
	Allium cepa	St, B, L, PM	Kuchy et al., 2016

(Continued)

TABLE 1 | Continued

Factor	Species	Phenotype*	Reference
Fungicide	*Hordeum vulgare*	St, B, F, M	Wuu, 1967
		↓CO	Bennett, 1971
		↓CO	Sharma et al., 1983
	Allium cepa	St, B, F, M	Mann, 1977
		St, B, L, M	Fisun and Rasgele, 2009
		St, B, L, PM	Kuchy et al., 2016
	Pisum sativum	↑↓CO	Choudhary and Sajid, 1986
	Capsicum annuum	St, B, L, U, multivalents	Prakash et al., 1988
	Lathyrus sativus	S, B, L, F, U	Kumar and Sinha, 1991
Heavy Metals	*Glycine max*	St, L, U, B, PM	Kumar, 2007
	Zea mays	PM, B, L, U, F, M	Kumar and Rai, 2010
	Vicia faba	St, L, B	George, 2000
	Hordeum vulgare	PM, L, B, M	Mittal and Srivastava, 2014
	Lathyrus sativus	U, ↓CO	Kumar and Ritambhara, 2006
		St, Sp, L	Tripathi and Girjesh, 2010
	Capsicum annuum	St, PM, L, B, F, M	Aslam et al., 2017
	Vicia faba	S, St, L, B	George, 2000
Caffeine	*Secale cereale*	L, B, ↓CO	de la Peña et al., 1981
	Trigonella foenum-graecum	L, B, U, St, PM	Anis and Wani, 1997
Pathogen	*Oryza sativa*	↑CO	Si et al., 2015
	Carica papaya	L, B, U	Pandey, 2017
	Datura quercifolia	↓CO, U, L, M	Kaul, 1968
	Solanum lycopersicum	PM, A	Caldwell, 1952
	Capsicum annuum	↓CO, Sp	Swaminathan et al., 1959
	Lycopersicon esculentum	B, PM, M, F	Andronic, 2012
	Hordeum vulgare	B, PM, L	Andronic, 2012
Antibiotics	*Allium cepa*	St, L, P, B, F	Mann, 1978
	Lathyrus sativus	U, St, B	Kumar and Sinha, 1991

**CO, change in crossover rate; St, stickiness; L, laggards; B, bridges; F, fragments; U, univalents; A, aneuploidy; M, micronuclei; PM, precocious movements; Sp, spindle aberrations. ↑ denotes increase, ↓ denotes decrease.*

in this species, this phenomenon has important implications for cracking open tight linkage groups, which are otherwise refractory to recombination events. These observations were confirmed by a subsequent study (Phillips et al., 2015), which went on to show that high temperature increases only class II CO frequency in male meiosis, and also demonstrated that interstitial regions of the genome are more prone to these changes. There is a tantalizing prospect, therefore, that simple heat shocking of barley at vulnerable stages of development could release potentially useful genetic variation for use in advanced breeding programs. However, this is predicated upon a greater understanding of the genetic (see review by Wang and Copenhaver, 2018) and epigenetic processes (reviewed by Yelina et al., 2015) underpinning these effects, which could ultimately enable the precise reprogramming of the crop.

The variation in response to temperature, even within the same species, may indicate that there is plasticity in the mechanisms governing CO control, or may implicate alternative pathways with different mechanisms. A caveat is that these differences may simply reflect discrepancies in the methods used to acquire and compare data, as has been inferred by (Wilson, 1959a; Bomblies et al., 2015; Lloyd et al., 2018).

Whilst temperature effects on recombination are the most widely described in the literature, there is some information describing other abiotic factors of relevance to climate change. Water stress has been shown to cause meiotic chromosome abnormalities in rice, such as laggards, micronuclei, univalents and a partial arrest of meiosis at severe stress levels (Namuco and O'Toole, 1986). In water stressed barley, abnormal chromosomal pairing and segregation during meiosis was found, leading to loss of pollen fertility (Skazkin and Zavadskaya, 1957). Cytological studies in *Sesbania* pea found that waterlogging stress resulted in various chromosomal aberrations and a reduction in pollen fertility (Srivastava and Kumar, 2016). Verde (2003) has also presented evidence that meiotic recombination increases in response to droughting in two genotypes of maize (*Zea mays*). van Tol et al. (2018) detected a 70% increase in recombination frequency between markers in response to salt stress of *Arabidopsis,* and genotyping revealing that CO fluctuation was not limited to the region between the marker genes but occurred throughout the genome. Modliszewski et al. (2018) did not detect the same effect under similar conditions in the same species. Considering that elevated CO_2 levels is one of the most prominent causes of climate change, it is surprising that little research has been conducted to examine its influence

on meiosis. Koti et al. (2005) showed no effect of elevated CO_2 on pollen viability in *Glycine max*, inferring that meiosis was also unaffected.

AGRICULTURAL INPUTS

Innovations that emerged during the 'Green Revolution' led to a steady rise in agricultural output across the globe (Tilman et al., 2002). These gains were driven principally by the development of new crop varieties and through the increased use of inputs, namely synthetic fertilizer and pesticides. The benefits of these inputs to crop productivity are clear and well documented, as are the negative impacts on the adjoining environment. Agricultural pollutants can influence natural non-target plant populations in close proximity via direct contact (e.g., spray drift), or may affect a much larger area via groundwater contamination (Moss, 2008).

FERTILIZER

The global demand for fertilizer nutrients (N, P_2O_5, and K_2O) has increased steadily since the 1960s, and is predicted to increase from 184.02 million tons in 2015 to over 200 million tons in 2020 (Food and Agriculture Organization [FAO], 2017). It has long been recognized that nutrient state influences meiotic processes. One of the first studies used a sterile F_1 hybrid between *Gilia millefoliata* and *G. achilleaefolia,* and observed that plants grown in rich loam had consistently higher bivalent frequencies, more chiasmata per bivalent on average, and fewer anaphase bridges than those grown in sand (Grant, 1953). Later, Griffing and Langridge (1963) determined the optimal growth conditions for elevated levels of recombination in tomato, a key component in commercial breeding programs. They observed that the CO frequency for a known interval decreased from 17 to 6% over a 6 months period during which no additional fertilizer was supplied. Subsequent addition of fertilizer restored the CO frequency to 12%, implying that nutrient-rich conditions enhance the rate of CO (Griffing and Langridge, 1963).

Subsequent investigations used a more systematic approach in order to isolate particular components, which had the greatest influence on meiosis. In an early example of such an approach, Law (1963) determined the influence of high and low concentrations of potassium and calcium on chiasma frequency in *Lolium temulentum* grown at both 20 and 30°C. High potassium increased chiasma frequency at both temperatures, and reduced its variance in the high temperature regime (Law, 1963). Bennett and Rees (1970) observed subsequently the same phenomena in rye (*Secale cereale*) grown under high phosphate conditions, recording higher chiasma frequencies and lower variance compared with controls. One of the most detailed studies of the effects of phosphate was conducted in *Arabidopsis* by comparing the recombination rate between pairs of genes conferring resistance to kanamycin and hygromycin (Barth et al., 2000). Under 10-fold higher levels of phosphate, recombination between loci on chromosomes 1 and 2 was significantly reduced, whilst intervals on chromosomes 4 and 5 showed minor, non-significant increases in recombination.

High phosphate also has a notable effect on a desynaptic barley mutant, enhancing the formation of chiasmata to 10.6 per cell compared to 7.7 for the control (Fedak, 1973). In a subsequent study, Dhesi (1975) noted a significant increase in chiasmata at metaphase I in a desynaptic mutant of pearl millet (*Pennisetum glaucum*) subjected to elevated levels of phosphate or potassium. However, elevated phosphate does not influence recombination in all species, such as soybean (*G. max*) (Hanson, 1961).

All of the studies described above used diploid plant species. However, Grant (1953) reported that bivalent frequency dramatically increases in a neoallotetraploid formed from the hybridisation between *G. millefoliata* and *G. achilleaefolia* when watered with a solution of mineral nutrients. Autotetraploid rye grown in Hoagland's solution II containing nitrogen has a higher quadrivalent frequency, at the expense of bivalent formation, and the same number of chiasmata compared to plants grown without nitrogen (Hossain, 1978). More recently, Hoagland's solution has also been shown the significantly increase CO formation in wheat and wheat-rye hybrids lacking the *Ph1* locus, which suppresses COs between homoeologs (Martín et al., 2017). A subsequent study showed that the magnesium in the Hoagland's solution was responsible for the observed phenotype (Rey et al., 2018).

PESTICIDES

Crop protection agrochemicals are another cornerstone of modern agriculture and are essential for minimizing yield losses. In 2015 alone, a total of 2,752,759 tons of active product was applied to crops globally, predominantly as herbicides, fungicides, and insecticides (Food and Agriculture Organization [FAO], 2018[2]). The influence of each of these pesticides groups on meiosis has been assessed (Sharma and Panneerselvam, 1990) and key examples are highlighted below.

One of the earliest studies to examine the influence of herbicides on meiosis was conducted by Wuu and Grant (1966). Barley seeds were soaked in 3-(3,4-dichlorophenyl)-1-methoxy-1-methylurea for 24 h prior to sowing, and meiocytes collected from the treated plants were analyzed cytologically. The authors documented numerous defects such as chromatin bridges, micronuclei, and asynchronous division. Sharma et al. (1981) examined the influence of three additional herbicides, bromacil, lenacil, and terbacil, all applied to barley seed at various concentrations for 6 h. Treatment with terbacil significantly reduced the chiasma frequency and was as disruptive as ethyl methanesulfonate (EMS), which was included as a control compound. The susceptibility of meiosis in *V. faba* to 2, 4, 5-trichlorophenoxyacetic acid (2,4, 5-T), 2, 4-dichlorophenoxyacetic acid (2, 4-D) and 2, 4-dichlorophenol, an intermediate product in the degradation pathway of 2, 4-D, was assessed by Amer and Ali (1974). The compounds were applied to both seed and sprayed onto 15 and 35 days old plants. Treatment at 35 days with 2, 4, 5-T led to the highest levels of sterile pollen grains resulting from stickiness, lagging chromosomes, and chromosome fragmentation during meiosis.

[2]http://www.fao.org/faostat

Badr et al. (1987) reported terbutryn also induced chromosomal abnormalities in 11.3% of cells undergoing meiosis in *V. faba*.

Liang et al. (1969) sprayed sorghum (*Sorghum vulgare*) plants that ranged between 5 and 20 cm in height with atrazine (2-chloro-4-ethylamino-6-isopropylamino-s-triazine), 2,4-D, alkanolamine salts of 2,4-D, and non-phytotoxic petroleum oil (crop oil), or their combinations. All increased the level of cytological aberrations at meiosis, including inducing aneuploidy and polyploidy. Two further studies assessed the influence of atrazine on meiosis in sorghum. Lee et al. (1974) also found a high degree of meiotic abnormalities in atrazine-treated sorghum, while a subsequent study noted more subtle changes to the meiotic nuclear landscape; additional nucleoli were frequently observed at diplotene and early diakinesis in treated plants (Currie and Liang, 1996). Soriano (1984) also reported the influence of a herbicide, whose active ingredient is N-(butoxymethyl)-2-chloro-2′, 6′-diethyl-acetanilide, applied at concentrations of 0.05–0.20% to sorghum seed. The lowest concentration induces aneuploidy in 2.9% of metaphase I cells, increasing to 8.8% at the highest concentration, compared to 0% in untreated plants. Interchanges, bridges and fragmentation were observed during meiosis I only at the higher concentrations.

The herbicide maleic hydrazine was applied to seed of *Helianthus annuus* at concentrations of 10^{-5} M to 10^{-2} M to determine its meiotic influence (Kaymak, 2005). This study reports not only a significant increase in abnormalities during both the first and second meiotic divisions, even at the lowest concentration tested, but also identifies a significant degree of abnormalities in the subsequent generation. A more recent study by Singh and Srivastava (2014) tested the effect of glyphosate and pendimethalin applied to the foliage of *Vigna mungo* 21 days from the point of sowing. They noted numerous defects, including chromatin bridges, laggards at anaphase I, disturbed spindle formation and binucleate cells in 17% and 21% of pollen mother cells (PMCs) treated with pendimethalin and glyphosate, respectively.

The influence on meiosis of a wide range of insecticides has been assayed in *V. faba* (Amer and Farah, 1968, 1976, 1980, 1983; Amer and Ali, 1983). In one of the earliest studies, Amer and Farah (1968) applied *N*-methyl-1-naphthyl-carbamate over various timeframes. After a single application, 8.7% of PMCs contained an aberration at diakinesis and metaphase I, compared to 1% in the control, rising to 23% if applied daily over a 7-day period. Defects were also later observed at anaphase I, metaphase II, and anaphase II (Amer and Farah, 1968). In *V. faba* both *O*,*O*-dimethyl-*N*-methyl-carbamidomethyl dithiophosphate and *O*-isopropyl-*N*-phenyl carbamate applied to seed prior to planting or sprayed (on day 15 or 35) induced multipolar anaphase II, along with a host of other types of meiotic abnormalities, the effects of which did not influence the yield phenotype of the successive two generations (Amer and Farah, 1976). One of the most profound effects was noted for the organophosphate insecticide chlorpyrifos (0,0-diethyl 0-3, 5, 6-trichloro-2-pyridyl phosphorothioate). When applied as a spray to seedlings or at the flowering stage the result was the same; chromosome stickiness was observed in more than 80% of the abnormal meiocytes (Amer and Farah, 1983). A single application during flowering of another organophosphate, methamidophos (0,*S*-dimethyl phosphoramidothioate), was sufficient to significantly increase the number of abnormal PMCs to 8.4%, compared to 1% in the control (Amer and Farah, 1987). Repeat application exacerbates the effect, causing abnormalities in 21% of PMCs.

The meiotic influence of four organophosphorus insecticides applied to *Capsicum annuum* was assessed by Devadas et al. (1986). The insecticides, namely dimethoate, DDVP, phosphomidon and monocrotophos were applied to seed at concentrations of 0.1, 0.5, and 1.0% for 24 h. Each treatment depressed pollen viability, with the degree of sterility rising with increasing concentration. The sterility is caused by univalents, multivalents, bridges, lagging chromosomes, non-synchronization, multipolar formation, micronuclei, unoriented and unequal disjunction of chromosomes identified in the preceding meiosis. The authors also claim that the insecticides tested are as disruptive as ionizing radiation. Reddy and Rao (1981), also working with *C. annuum*, focused on two different compounds, BHC and Nuvacron, the latter being a organophosphorus systemic and contact insecticide. The compounds were applied at a range of concentrations to both the seed and sprayed on plants at fortnightly intervals. Both were found to induce abnormalities during meiosis, ranging from 3.1 to 5.6% for BHC and 7.7–15.6% for Nuvacron. The authors note that the lowest concentration is favored by Indian farmers at the time of publication. A later study by Lakshmi et al. (1988) examined the influence of Ekalux EC 25 [0-diethyl-o-(quinoxylinyl-2) phosphorothionate] and Metasystox (oxydemeton-methyl = S-(2(ethyl-sulphinyl)-ethyl) & 0, 0-dimethyl phosphorothioate), applied to seed of *C. annuum* followed by four spray applications during growth. This study is one of few to score chiasma frequency, and noted a steady decline in COs with increasing concentration of each insecticide. COs were reduced to the lowest number of 21.08 for Ekalux EC 25 and 20.5 for Metasystox, compared to 23 in the control. Other meiotic defects including laggards, bridges, stickiness and univalents were also noted in this study.

Kuchy et al. (2016) examined the effects on *A. cepa* of an organophosphate insecticide containing dichlorvos (2,2-dichlorovinyl dimethyl phosphate) and a organochlorine insecticide, endosulfan. The organophosphate compound was the most potent at inducing abnormalities, affecting 11–27% of PMCs depending upon which concentration was applied, compared to 3% in the control. Endosulfan also caused numerous meiotic failures, with 9–20% PMCs containing defects, depending upon the concentration used. The most common abnormality observed was stickiness at metaphase I and II.

One of the earliest investigations of the influence of fungicides on meiotic recombination was conducted by Bennett (1971) who tested Ethirimal (5-butyl-2-ethylamino-4-hydroxy-6-methyl pyrimidine), a systemic compound applied as a seed dressing in barley. The mean chiasma frequency in each of three cultivars was significantly reduced to 2–4% lower than the control. A later study in the same species showed that the systemic fungicides fuberidazole, carboxin, and oxycarboxin (but not thiabendazole) all significantly reduced chiasma frequency (Sharma et al., 1983).

Carboxin and oxycarboxin has an effect even at the lowest concentration tested.

The transgenerational effect of the fungicide carbendazim (2-methoxy-carbamoyl benzimidazole), was studied in two different cultivars of *Pisum sativum* (Choudhary and Sajid, 1986). Plants were sprayed four times during development with the recommended dose of 0.2% aqueous solution, and at 0.4%. Both concentrations significantly altered the chiasma frequency, with one cultivar being more susceptible, implying a genotypic interaction with the fungicide. The subsequent two generations of the treated plants, which received no further applications of fungicide, also had a significantly altered CO landscape, one cultivar having fewer COs contrasting with the second which had more. Abnormalities such as stickiness, fragmentation and micronuclei, were also observed in PMCs of *A. cepa* treated with either one of four different Dithane based fungicides or treated with carbendazim (methyl-2-benzimidazole carbamate-MBC) (Mann, 1977; Kuchy et al., 2016). Fisun and Rasgele (2009) treated *A. cepa* bulbs with roots 1.5–2 cm in length with different concentrations (1800–6000 ppm) of the fungicide tebuconazole, for 3–24 h. All treatments resulted in a significant increase in meiotic abnormalities, including a significant increase in the number of quadrivalents, believed to be a result of chromosome translocations.

OTHER ANTHROPOGENIC INFLUENCES

Whilst environmental stresses and agricultural pollutants commonly affect meiosis in plants, there are also a number of other anthropogenic factors that can have a similar effect. As the human population increases and encroaches upon the global natural environment, the trail of anthropogenic influences grows commensurately. Increasing agricultural and industrial developments expose plant populations to new and different chemical and physical agents and places them in environments that can potentially alter their development. There is greater pollution from industrial and automotive combustion, commercially and pharmaceutically used solvents, additives, chemicals and an increase in pathogen prevalence worldwide (Evans et al., 2008; Gaffney and Marley, 2009; Tornero and Hanke, 2016).

HEAVY METALS AND COMBUSTED GASSES

Heavy metal contamination of the environment is increasing due to human activity, with many sources of pollution primarily entering water courses and polluting the land. The accumulation of heavy metals and metalloids in soil also originate from other sources, such as emissions from industrial areas, leaded fuels and paints, sewage sludge, biosolids, animal manures, spillage of petrochemicals and combustion residues (Khan et al., 2008; Zhang et al., 2010).

Samples of agricultural soils from the siling reservoir watershed in Zhejiang Province and an area of north east China that has been of intensively farmed for decades were found to contain high levels of cadmium contamination (Naveedullah et al., 2013; Shan et al., 2013). At some metalliferous sites there can be 100 times elevated metal concentrations in the soil compared with uncontaminated areas (Bert et al., 2002). Soil samples from agricultural areas of Jiaxing, a rapidly industrializing area in the Yangtze Delta of China, has localized hot spots of pollution of copper, zinc, lead, chromium, nickel and cadmium (Xu et al., 2014). The concentrations of the heavy metals lead, copper, cadmium, and zinc can be further increased by urban runoff or combustion sources, and copper, chromium and tin levels even further increased by automobile break and tire wear (Davis et al., 2001; Hulskotte et al., 2007; Shan et al., 2013). Another surprising pollution source are shooting ranges as the soil there often has higher levels of antimony, nickel, lead, copper and zinc and can be used for animal grazing when not in use or decommissioned (Robinson et al., 2008; Bannon et al., 2009).

There may be no cause for concern for some current levels of heavy metal contamination of the soil, and potentially the food chain, as they may often be below the acceptable thresholds for safe human consumption. There is, however, reason to investigate what effects they may have on the recombination landscape of the plants and crops that grow in these areas, as heavy metals are known to effect plant development in a number of ways. *Arabidopsis* plants treated with 50 or 100 mM copper, cadmium or nickel have at least a twofold increase in somatic homologous recombination frequency with successive treated generations exhibiting even higher increases (Rahavi et al., 2011). This study also found that the subsequent generation, which was not exposed to any stress, still possessed significantly higher residual rates of recombination when compared to the non-exposed progeny. Further studies found that chromosomal abnormalities, including chromosomal bridges, scattering and precocious movements occurred in *G. max* and *Z. mays* when treated with cadmium (Kumar, 2007; Kumar and Rai, 2010). Similar results were found when *H. vulgare* was treated with a combination of cadmium and chromium. This combination treatment also resulted in a significant decrease in the number of pollen grains per anther and a significant increase in pollen sterility (Mittal and Srivastava, 2014).

Although the current known levels of heavy metals found in soils due to anthropogenic influences may not be enough to modify the recombination landscape alone, there are other agents, such as anthropogenic gasses, that are known to have detrimental effects on plants. A cytogenetic test based upon quantifying micronuclei resulting from chromosome breakage in meiotic pollen mother cells *T. paludosa* (Trad-MCN) has found that various anthropogenic gasses such as NO_2, SO_2, O_3, HN_3, and EMS have clastogenic effects. Both gaseous HN_3, and EMS were clastogenic after 6 h exposures while SO_2 and NO_2 required 22 and 24 h, respectively (Ma et al., 1982; Rodrigues et al., 1996). Several indoor environments containing pipe and tobacco smoke, and formaldehyde fumes were found by the Trad-MCN assay to cause chromosomal breakage, as well as several outdoor locations such as parking garages, truck and bus stops, agrochemical industrial sites, a P-dichlorobenzene treated

herbarium and an industrial site (Ma et al., 1980, 1982; Ma and Harris, 1987a,b). Although this only shows that *T. paludosa* can be clastogenically affected by anthropogenic environments, it emphasizes the unintended consequences of human activities.

Heavy metals and combusted gasses in the environment are not the only anthropogenic sources that could change the recombination landscape of crops around the world; there are also large amounts of pharmaceutical chemicals that pass into the environment and to the soil.

PHARMACEUTICAL CHEMICALS

As pharmaceutical drug use increases worldwide, there is growing concern for the high level of pharmaceutical residues in aquatic environments (Uslu et al., 2013). Treatment plants are not always able to remove pharmaceutical residues from sewage completely and often release amounts into the receiving waters (Heberer, 2002; Gaw et al., 2014; Küster and Adler, 2014; Zhang et al., 2016). While a large part of the concern comes from the potential of these residues to affect aquatic life and enter the drinking water supply, there is justification to question the effects they could have on plant life when treated biosolids are applied to agricultural land.

Extremely low levels of the anti-cancer drug bleomycin, known to cause an increase in DSBs and increased somatic recombination, have been found at concentrations of 11 – 19 ng/L and <5–17 ng/L in sewage treatment effluent and rivers, respectively (Aherne et al., 1990). Whilst these doses are well below the normal chemotherapeutic doses administered (20–30 mg/m^{-2}), data are sparse concerning the bioaccumulation of bleomycin or the amount that it is used worldwide. Qi et al. (2014) showed that 98 tons of pesticides, 152 tons of pharmaceuticals, 369 tons of polycyclic aromatic hydrocarbons and 273 tons of household and industrial chemicals are flushed annually into the East China Sea by the Yangtze river. This level of pollution could potentially affect meiotic recombination in plants, but virtually no investigations have been undertaken. The recent significant increase in drug-resistant bacterial strains is often attributed to the indiscriminate use of antibiotics by today's society. However, there should perhaps also be concern about the bioactivity of waste antibiotics in the environment. Some antibiotics in water courses and agricultural land are known to affect plants. For example, ciprofloxacin has been found in municipal waste water (Lee et al., 2007) and in soil samples (Golet et al., 2002; Goulas et al., 2016) and is known to cause double strand DNA breaks in *Arabidopsis*, (Rowan et al., 2010). Ciprofloxacin's bactericidal action comes from the inhibition of topoisomerase II (DNA gyrase) and topoisomerase IV, required for various bacterial DNA processes including replication, transcription, repair, strand supercoiling repair, and recombination (Aldred et al., 2014), and a recent study found that ciprofloxacin targets *A. thaliana* gyrase (Evans-Roberts et al., 2016). Tetracycline has been shown to induce meiotic aberrations including stickiness, laggards, bridges, and fragments in *A. cepa* (Mann, 1978), and has been found in soil fertilized with liquid manure and in soil and water near intensive commercial livestock operations (Hamscher et al., 2002; Thiele-Bruhn, 2003).

The increase in anthropogenic chemicals in the environment is not limited to pharmaceuticals, but also applies to chemicals resulting from human consumption. Caffeine can be found in soil due to the reuse of treated wastewater for irrigation (Bruton et al., 2010; Williams and McLain, 2012). Anis and Wani (1997) found that caffeine-treated populations of *Trigonella foenum-graecum* exhibited several meiotic abnormalities including laggards, univalents, bridges, stickiness, and precocious chromosome movements. A 0.1% caffeine solution was administered to *S. cereale* and abnormalities such as laggards, bridges and fragments and decreased chiasma frequency were observed (de la Peña et al., 1981). The widely used chemical bisphenol A (BPA) affects microtubule arrays of meristematic root-tip cells of *P. sativum* resulting in the stalling of cytokinesis, deranged interphase and mitotic microtubule arrays, and abnormal chromosome segregation (Adamakis et al., 2013).

PATHOGENS

The full impact climate change will have on the prevalence and spread of virus disease epidemics in natural vegetation and cultivated plants and crops is still unknown. Research suggests that elevated environmental CO_2 levels can alter hormone production in plants and precipitate the observed shift in susceptibility to insect herbivores and pathogens (Casteel et al., 2012; Zhang et al., 2015). Whilst research to understand the possible effects of some common climate change scenarios is ongoing, reviewed extensively in Jones (2016) and Trebicki et al. (2017), we still do not know what impact climate change may have on the recombination landscape of plants. Climatic changes are compounding the threat of spread of plant pest and diseases. A recent analysis indicated that crop pests are moving 2.7 km poleward annually and that on average, 10% of the major plant pests and disease agents have already infested half of the countries that they potentially could infect (Bebber et al., 2013, 2014). *Carica papaya* infected with papaya ring spot virus exhibited an increase in laggard chromosomes, and had a lower mitotic index and worse pollen viability compared to its healthy counterpart (Kumar Ravindra, 2017). Infection of *Arabidopsis* with the oomycete pathogen *Peronospora parasitica* has been shown to lead to an increase in somatic recombination frequency (Lucht et al., 2002). Interestingly, when Molinier et al. (2006) treated *Arabidopsis* with flagellin, an elicitor of plant defenses, they found that not only did somatic homologous recombination increase in the treated individual but also in successive generations. *Nicotiana tabacum* treated with the tobacco mosaic virus behaves in a similar way; somatic recombination increased in both the subject and its offspring, with one study showing that the offspring even exhibited a delay in symptom development when infected with viruses (Kovalchuk et al., 2003; Kathiria et al., 2010). Si et al. (2015) found that in some of the F_2 generation of *O. sativa* treated with rice blasts spores there was a significantly higher number of CO events compared to the controls. *Datura quercifolia* treated with mosaic virus resulted in a drastic decrease

in chiasma frequency, and the presence of univalents led to many irregularities such as laggards, micronuclei and a significant reduction in pollen and seed fertility (Kaul, 1968). Caldwell (1952) noted that *Solanum lycopersicum* treated with mosaic virus led to the breakdown of meiosis and in some instances cells forming with an irregular number of chromosomes. Yao et al. (2013) found that a local infection of either tobacco mosaic virus or oilseed rape mosaic virus leads to a systematic increase in somatic homologous recombination frequency, with older plants having a higher recombination frequency than younger plants. *Lycopersicon esculentum* and *H. vulgare* infected with barley stripe mosaic virus exhibited an increase in various chromosome abnormalities and a shift in chiasmata toward the interstitial regions (Andronic, 2012). Anthropogenic influences resulting in a changing climate can lead to an increased level of viral vectors and more disease epidemics in plants worldwide, but they could also be enough to change the meiotic recombination landscape forever.

LIMITATIONS OF CURRENT STUDIES

As outlined above, there is a wide range of anthropogenic factors that have been shown to cause various meiotic abnormalities. In the vast majority of cases, the precise biochemical action induced by the treatment during meiosis has not been ascertained; temperature is the notable exception (see earlier section for detail). Many studies reported abnormal meiocytes with chromosome stickiness, bridges, fragmentation and micronuclei. However, it is yet to be determined if the factors themselves are clastogenic and cause DNA damage directly, or whether they interfere with the repair of double strand breaks (DSBs) formed naturally during prophase I. Cytology of fixed meiotic material was by far the most prevalent method of determining the extent of meiotic abnormalities induced by each treatment, and in most studies only gross changes were recorded. More subtle influences, such as changes in chiasma frequency at metaphase I, were recorded in only approximately a third of the studies summarized in **Table 1**. The scoring of chiasmata is not sensitive and cannot detect small changes in recombination frequency, making it likely that more subtle effects at the lower concentration range were not detectable.

The biochemical pathways affected by these treatments may be elucidated by studies in non-plant species. Allard and Colaiacovo (2010) used *Caenorhabditis elegans* to analyze the meiotic molecular pathways affected by BPA. They showed that BPA perturbs both synaptonemal complex and chromosome integrity during pachytene, and also alters DSB repair progression and activation of the DNA damage checkpoint. The effect of the herbicide atrazine on meiosis has been studied in both male and female mice (Gely-Pernot et al., 2015, 2017). In male mice, atrazine reduced sperm count by 68%, caused by a delay in meiotic progression arising from the persistence of unrepaired DSBs (Gely-Pernot et al., 2015). The study also found that the herbicide affects the expression of genes involved in mitochondrial function, steroid-hormone function and GTPase activity, and also altered the pattern of histone H3 trimethylation at lysine 4 (H3K4me3). A subsequent study switched focus to female meiosis and found that atrazine increased the level of oxidative stress in the nuclei of meiotic cells, as measured by the level of 8-oxo-guanine, which affected DBS repair, synapsis and CO frequency (Gely-Pernot et al., 2017).

Another shortcoming of most published studies is that the concentrations of the chemical treatments used cannot be related to those used in agriculture or experienced by plants in natural environments. The biological significance, in terms of potential threat to the meiotic process, is therefore difficult to ascertain. Taking agricultural inputs as an example, a number of agrochemicals have been subsequently banned or their application drastically reduced. The persistence of these substances in the environment also varies, and may have the potential to affect plant communities long after their last application. For example, atrazine was first introduced as a herbicide in 1958 but was subsequently withdrawn from use in most Northern European countries in the early 1990s, and banned from the whole European Union in 2004. Traces of atrazine are still detectable in soil sampled from agricultural land in Germany where the last application was prior to 1991, and in marine sediments of the Mediterranean (Noedler et al., 2013; Vonberg et al., 2014).

In the majority of studies cited, only one treatment was applied to a single plant species that was grown under controlled conditions. This is starkly different to reality where multiple xenobiotics, abiotic and biotic stresses may impact together in one environment. To date, only one published study examines the impact on meiosis of plant species growing in polluted environments. Zohair et al. (2012) sampled 14 species belonging to the Cyperaceae and Poaceae growing in the vicinity of industrial sites and agricultural fields around Karachi, Pakistan, and compared them with their counterparts in unpolluted environments. All of the plant species collected from the contaminated sites had significantly higher numbers of aberrant PMCs with precocious movement, stickiness, aberrant spindles or lagging chromosomes. The prevalence of abnormal PMCs varied greatly between species; the largest effect was observed in *Cyperus arenarius* where 99% of PMCs contained defects, compared to 13% for the control, contrasting with *Ochtochloa compressa* where only 7% of PMCs were defective, compared to 2% in the control. The study also identified an elevated number of unreduced dyads and sterile pollen grains.

Numerous genetic modifiers of recombination have been identified. One of the first studies to note this was Gale and Rees (1970) who observed small but significant differences in chiasma frequencies in five *Hordeum* species, attributed to genotypic variation in the populations. Ziolkowski et al. (2017) identified that 56.9% of CO variation in a F_2 population from a cross between two *Arabidopsis* accessions, Columbia and Landsberg, was caused by semi-dominant polymorphisms in *HEI10*, a conserved ubiquitin E3 ligase. Interaction between such genetic elements and environmental variables has not been extensively studied. Rezaei et al. (2010) noted an interaction between the extent of meiotic irregularities and environmental conditions in *Tritium turgidum*. Zheng et al. (2014) reported that

cyclin-dependent kinase G1 (*CDKG1*) was required for normal levels of synapsis and CO formation in male meiosis in *Arabidopsis*, but only at elevated temperatures.

The range of plant species assessed for their meiotic sensitivity to anthropogenic factors is very narrow and confined to angiosperms, and in most instances only those used in agriculture. Single species are usually examined as targets for agrochemicals, and most non-target species are ignored. The effects on angiosperms in non-agricultural habitats, such as woodlands or estuaries and other plant groups, such as gymnosperms, are less known because of the difficulties of experimenting with such species. One such study by Bykova et al. (2018) found that a 27% reduction in precipitation resulted in a 35% reduction in viable pollen grains compared to the control in male *Quercus ilex*. Most of the studies relate to male meiosis, so the sensitivity of the ovule is largely unknown. Hundreds of xenobiotic compounds have been assessed, including those tested by the *Tradescantia* Trad-MCN assay, but this represents a small fraction of the 10,000s of compounds present in the environment (Donner et al., 2010; European Psychiatric Association [EPA], 2018).

EVOLUTIONARY CONSEQUENCES

Empirical research has shown that both the number and distribution of recombination events are tightly controlled, and such non-random patterns have been shown to be stable through generations (see review by Stapley et al., 2017). In all plant species, there are regions of the genome that have few COs events; such regions are termed cold spots. The result of such linkage-disequilibrium is to maintain supergene groups, co-evolved loci or favorable linkage groups, which are of benefit to the plant. Alternatively, undesirable allele combinations could be maintained. As previously discussed, elevated temperature modulates the meiotic landscape of barley and *Arabidopsis* and disrupts linkage groups (Phillips et al., 2015; Lloyd et al., 2018; Modliszewski et al., 2018), which could alter the evolutionary fitness of the plants subjected to this stress.

Many of the anthropogenic stresses, including temperature, agrochemicals and fungicides were reported to cause spindle aberrations during the first and second meiotic division that in some instances gave rise to unreduced gametes and the potential for polyploidisation (Mason and Pires, 2015). High nutrient conditions aids the stabilization of neopolyploid and could drive the evolution of new polyploidy species. Xenobiotic compounds currently found in the environment have no equivalent in the history of our planet and therefore the long-term effect in terms of promoting polyploidy are unknown. The environmental climate of the planet has fluctuated on numerous occasions, and its impact on ploidy recognized. One such event occurred at the Cretaceous–Tertiary (KT) boundary that caused the mass extinction of many species, including about 60% of plant species, but drove the formation of polyploid species (Fawcett et al., 2009; Vanneste et al., 2014). Polyploidisation is believed to confer better adaptability and tolerance to altered environmental conditions, a trend that may be repeated in the current climate change cycle.

Plant speciation is often associated with structural changes in the genome resulting from aneuploidy, dysploidy, or other chromosome rearrangements such as translocations, inversions, fusions, or fissions (De Storme and Mason, 2014). None of the studies cited in this review report such structural changes, but none specifically set out to identify such morphological changes. Notable abnormal chromosome conformations, such as laggards, bridges, fragments, micronuclei, and aneuploidy are reported in many of the studies, and are capable of altering the genomic landscape of the subsequent generation.

SUMMARY

The influence of the human race on the natural environment is undeniable, ranging from altering climatic conditions globally to the local contamination with a specific xenobiotic compound. The influence of many such factors have been reported in a number of different angiosperms, with effects ranging from altered patterns of recombination to severe chromosome damage originating from stickiness and bridges. In most cases, only basic cytology has been used which has shed little light on the underlying mode of action of the factors. Many of the citations predate the development of the sensitive assays now available, and it would be profitable to use such methods to identify how these factors impinge upon on the biochemical pathways operating during meiosis, using concentrations of xenobiotics of relevance to plant populations. The long-term consequences of destabilizing the genome may have a profound evolutionary legacy.

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All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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