Challenging genome intergrity

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Plant breeders try to widen gene pools by making inter-generic and inter-specific hybrids and polyploids, by introgression breeding and by creating transgenic plants, and in the process they disturb the 'balance of nature' within the nucleus. The bringing together of alien genomes, or partial genomes, or the insertion of single chromosomes or genes into unfamiliar backgrounds can challenge the integrity of the genome and create a nuclear genetic conflict. The resolution of this conflict, including that caused by environmental stress, can proceed by several mechanisms:

- elimination of whole genomes
- genome restructuring in allopolyploids
- rapid changes in gene regulation and gene silencing in allopolyploids
- accommodating chromosome additions and substitutions
- gene silencing in transgenic plants
- environmental modulation of repetitive DNA.

We review this issue of nuclear genetic integrity in plants, and indicate ways in which it can be of advantage to breeders, or otherwise.

Key words: *Grasses, somatic recombination, chromosome elimination, allopolyploidy, genomic in situ hybridisation (GISH), genome restructuring*

INTRODUCTION

The idea of genome integrity has a long history. It was first considered by Heitz in 1928 [1], when he used constitutive heterochromatin in *Pellia endiviifolia* as a marker to track the coherence of chromosomes throughout the cell cycle. Heitz established that these markers could be seen at all stages of the cycle, and that the chromosomes retained their integrity during the interphase when they were not visible as discreet microscopic structures. Genome integrity as we now understand it includes the stably inherited components of a species, including the karyotype (number, size and form of chromosomes); the visible features of centromeres, NORs, telomeres, chromomeres, heterochromatic knobs (maize) and others parts which can now be identified by special staining procedures such as C- and G-banding and FISH. In addition, we imagine that DNA sequences, *viz.* genes, repetitive sequences, retroviral and transposon insertions, etc., also have permanence and provide for the integrity needed to make heredity work. The context is the timescale of human experience and the way in which human intervention compromises the natural order of the genome. In terms of evolutionary timescales genomes do change naturally, as we see in the plant kingdom where *Arabidopsis thaliana* has less than 1 pg of DNA in its 4C nuclear genome whereas *Fritillaria assyriaca* has more than 500 pg [2], and the grass species *Zingeria biebersteiniana* has a chromosome number of 2n = 2x = 4 while the polyploid apomict *Poa litorosa* has 2n = 38x = = 266 [3].

On a smaller scale there is also flexibility within species, as in the content of heterochromatin in lines of maize [4] or copy number of a family of dispersed repeats in *Vicia faba* [5]. The subject of genome integrity embraces both of the two kingdoms and could include prokaryotes as well. To give some focus to our review, we confine ourselves to the plant world and to matters which are mainly within our own experience and in the realm of plant molecular cytogenetics. The main focus is on newly made allopolyploids.

ELIMINATION OF WHOLE GENOMES

Wide crosses between different species, or genera, are well known as a means for forming doubled haploids for breeding purposes. Perhaps the best known system, of many, is that of *Hordeum vulgare* × *H. bulbosum*. Following pollination by the perennial wild *bulbosum* there is an immediate nuclear conflict in the diploid

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F_1 zygote. The conflict is resolved by elimination of the entire set of *bulbosum* chromosomes in the first few mitoses of the embryo. Embryo rescue and chromosome doubling then produces the doubled haploid of *H. vulgare*. The resolution to the challenge to genome integrity is thought to start as early as the first anaphase of the hybrid zygote, and is completed about five days later. The *bulbosum* chromosomes are located more to the periphery of the metaphase plates and have smaller centromeres. Centromere suppression, possibly associated with 'directed DNA methylation', could be a key component of the process [6–8]. The elimination is genotype-dependent and does not always occur so abruptly, so that hybrid plants are sometimes formed and subsequent elimination is slow and unpredictable in the somatic tissues [9]. A similar scenario could be described in many other hybrids (*e.g.*, wheat × × maize), and it represents an extreme challenge to genome integrity and its most violent and abrupt resolution. In this case the outcome has usefulness for the breeder, and by now there is a long list of varieties that were produced from these interspecific crosses where the alien pollinator species serve as haploid inducer of crops. Besides that, this system sometimes results in a much wished-for gene introgression. In dihaploid potato production Wilkinson et al. [10] have reported a robust case for somatic translocation in a euploid formed from the cross of *Solanum tuberosum* × *S. phureja*. Genomic *in situ* hybridisation (GISH) and Southern analysis confirmed that a segment of *S. phureja* (the inducer) chromatin was translocated into the *S. tuberosum* genome, possibly during the early development of the embryo.

GENOME RESTRUCTURING IN ALLOPOLYPLOIDS

Newly made allopolyploids often fail to perform to the expectations of breeders. They are typically unstable in terms of chromosomal rearrangements, in the number and distribution of their repetitive DNA sequences, and in various developmental abnormalities including fertility.

Jiang and Gill [11] have analysed several tetraploid wheat hybrids and have identified certain 'species-specific translocations' which appear in every population, and representing essential changes which are needed to meet genome challenge and to permit fertility and nucleo-cytoplasmic compatibility. Such species-specific intergenomic translocations have been reported in tobacco [12] and are also well known, for example, in allohexaploid *Avena sativa* [13]. According to Gill [14], newly formed hybrids experience a 'bottleneck of sterility', which results from adverse interactions between the nuclear genome of one of the parental species and the nuclear and cytoplasmic genome of the other parent species; and to overcome this sterility barrier certain cytogenetic changes have to occur in the nuclear genomes to restore fertility and genome balance in the hybrids.

Triticale

Hybrids between wheat and rye, to produce triticale after chromosome doubling, have been known since the 1930s to have a high frequency of meiotic disturbances which resulted in inferior aneuploid plants [15]. Triticale is a classic case of the loss of genome coherence following interspecific hybridisation. Failure of chromosome pairing is the main cause of disturbance and appears to be related to the quantity of heterochromatin carried in the rye genome. Some amelioration has been achieved by using parental lines of rye low in heterochromatin, although the mechanism by which pairing failure is brought about remains elusive. Notwithstanding these obstacles, the patient breeding of selected lines has resulted in a significant number of improved and useful varieties [16].

Genome balance in *Lolium–Festuca*

The *Lolium–Festuca* hybrids attract breeders as a valuable combination of two grasses showing vigorous growth and high adaptability to climatic stress. Commercial amphidiploid *Lolium–Festuca* varieties representing the new plant species *Festulolium braunii* [(K. Richter) A. Camus] have been produced by breeders in Wales, Germany, Czech Republic, Poland and Lithuania. Genome *in situ* hybridisation (GISH) analysis has proved to be especially useful for studying the component genomes of allopolyploids, and for monitoring the genome adjustments which take place following their formation. Changes to genome balance in an allopolyploid have been recently shown by a GISH study in the F_8 population of a tetraploid hybrid between *Lolium perenne* and *Festuca pratensis* [17]. Meiosis in the early generations, as shown by conventional staining with acetocarmine, was characterised as stable with a high level of bivalent formation. The GISH study, however, revealed that extensive recombination had taken place between homeologues of the two genomes, and that the balance of chromatin was not equal. The substitution of *Festuca*-origin chromosomes by those of *Lolium*-origin resulted in a mean of 17.9 *Lolium* and 9.7 *Festuca* chromosomes per genotype. In terms of chromatin amounts this equates to a mean length of 62.1% *Lolium* and 37.9% *Festuca*. Clearly the genome challenge had been dealt with by a change in the genome balance, over the eight cycles of sexual reproduction, in favour of the dominant *Lolium* genome. A new example of *Lolium*-dominant be-

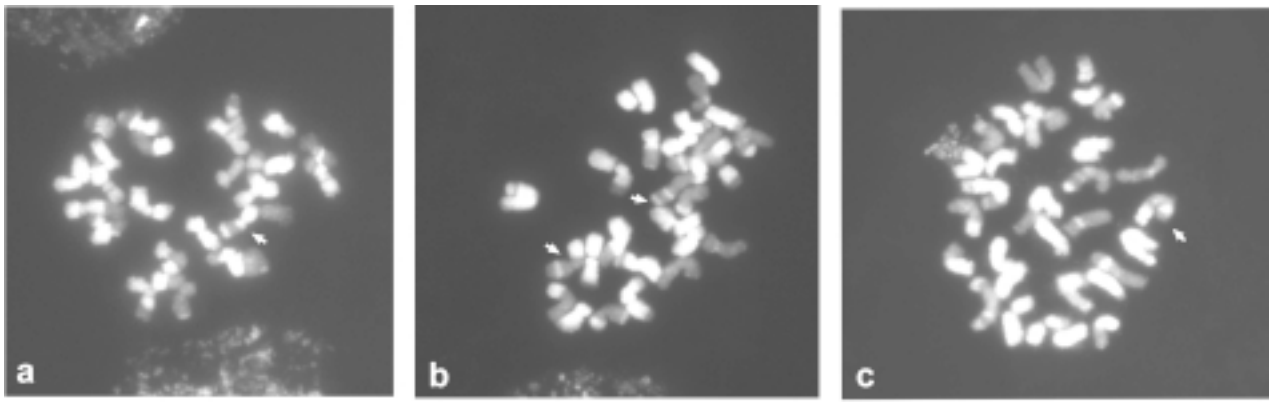

Fig. 1. Genomic *in situ* hybridisation (GISH) images of metaphase chromosomes from the Lithuanian tetraploid hybrid forage grass variety 'Punia' (*F. pratensis* × *L. multiflorum,* 2n = 4x = 28). GISH was carried out using a rhodamine-labelled probe prepared from total genomic DNA of *L. multiflorum* and counterstained with DAPI. Note the inter-genomic recombination (arrows); the rhodamine label indicates chromatin of *L. multiflorum* (light colour) and DAPI chromatin of *F. pratensis* (dark colour). The genome balance is in favour of *L. multiflorum*, and the difference between photos **a**, **b** and **c** shows genotype-dependent variation in the proportions of chromatin from the two constituent species. The variety has been grown by open pollination for 4 generations (photos from Izolda Pašakinskienė)

haviour has recently been found in the Lithuanian variety 'Punia' made from a cross at the tetraploid level of *F. pratensis* × *L. multiflorum* (Fig. 1.) Evidently the extent of inter-genome recombination and of chromosome substitution will vary depending on genotypes and on the species used. The mechanism involved in this particular form of genome interaction remains unknown, but some selection in favour of *Lolium* over *Festuca* at some stage of the life cycle looks likely.

Diploidisation and somatic recombination in *Lolium–Festuca*

Genome challenge involving newly made polyploids takes a novel form in the work described by Pašakinskienė et al. [18] and Pašakinskienė and Jones [19]. Crosses were made between diploid *Lolium multiflorum* (*Lm*, 2n = 2x = 14) and hexaploid *Festuca arundinaceae* (*Fa*, 2n = 6x = 42) to produce new hybrid forage grasses. The F_1 were obtained by embryo rescue and then treated with colchicine to double the chromosome number and to restore fertility in the amphiploids (2n = 8x = 56). Chromosome counts in the fertile hybrids revealed some unexpected diploid plants (2n = 2x = 14) as well as a number of the expected amphiploids with 2n = 56. Two different varieties of *Lm* were used, and in total there were 6 diploids out of the 30 plants tested (and 24 amphiploids). The breeding scheme is shown in Fig. 2. All six diploids displayed *festucoid*-like panicle inflorescences and therefore had the main diagnostic feature which distinguishes ryegrass (spike-like inflorescences) from fescue. The F_2C_1 generation was then produced from intercrosses among the fertile F_1C_0 and were assessed for their inflorescence type. The presence of the *Lm* inflorescence type is indicative of the hybrid origin of the F_1C_0 diploids, and this was found in 11 of the 52

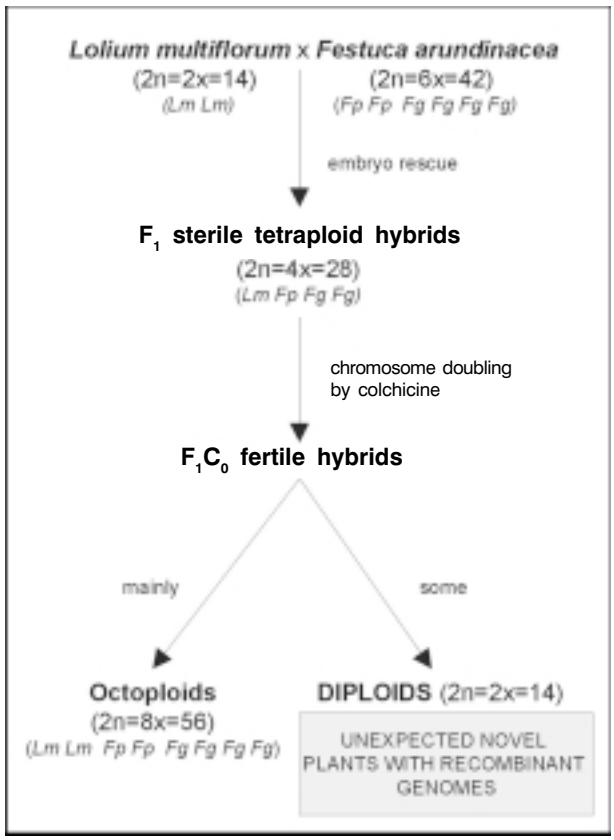

Fig. 2. Diagram showing the breeding scheme used to produce amphiploids from the cross of diploid *Lolium multiflorum* × hexaploid *Festuca arundinacea*, and the unexpected discovery of recombinant diploids among the fertile F_1C_0

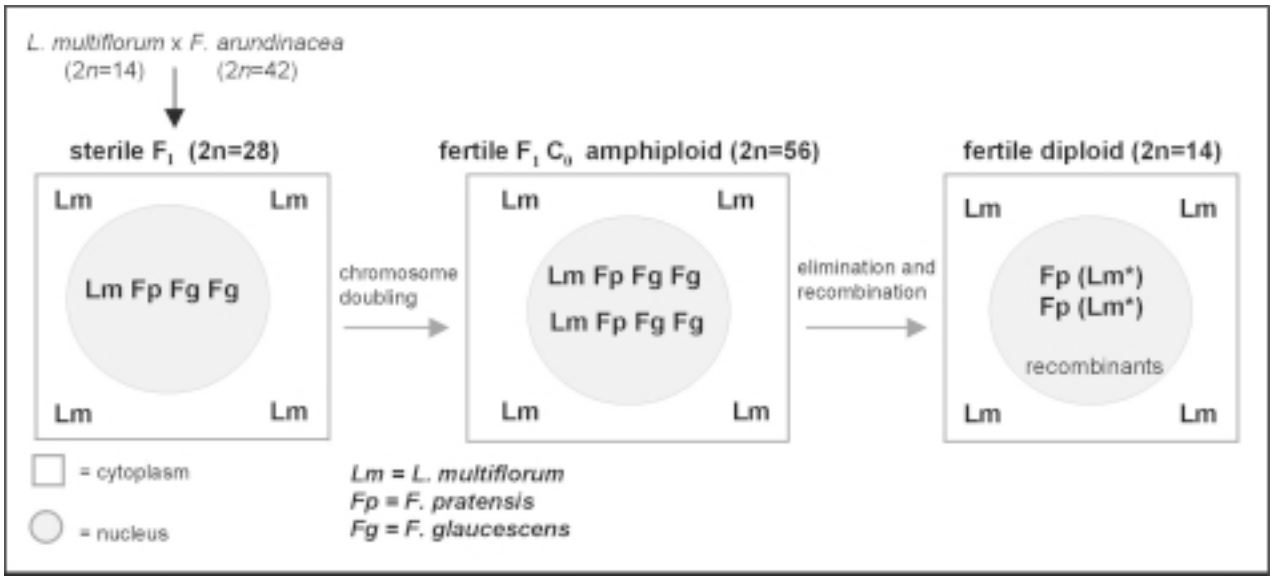

Fig. 3. Diagram showing the possible interactions within the nucleus and between the nuclear genomes and the cytoplasm in the polyploid hybrids between diploid *Lolium multiflorum* and hexaploid *Festuca arundinacea* (F_1 and F_1C_0), and the diploid which arises after chromosome elimination and somatic recombination (for genome constitution of *F. arundinacea* see Fig. 2)

F_2 plants available for study. It was clear that the novel diploids arising from the octoploid hybrids must contain variable amounts of genetics material from the original *Lm* parent. The fact that chromosome elimination had taken place to produce the diploids was not altogether surprising, given what we know about haploidisation in wide crosses, but it was unexpected to find that the diploids had new combinations of *Fa* and *Lm*.

Chromosome painting by the GISH technique revealed genome recombination in these 'novel diploids'. New genomes represented a mixture of chromatin from more than one genome; and it has to be remembered that the effects seen occurred in the diploid plants arising directly from cultured embryos and that no sexual progeny are involved. Cells were found with varying amounts of the *Lm* genome in the background of the genomic component coming from *Fa* (possibly *Fp*) as the main constitutive component. The genome challenge presented in the amphiploid hybrid is a complex one, as the scheme in Fig. 3 shows, and involves interactions between three genomes as well as between nucleus and cytoplasm. Its resolution is dramatic and takes place instantly in some genotypes during the development of the F_1C_0 plants. The hypothesis proposed was that these recombinants arose from two processes (genotype-dependent) going on in some of the unstable octoploid amphiploids: genome elimination to return to the diploid level, and somatic recombination. Another possible explanation of such a phenomenon is that of concerted transposition, which might be mediated as a consequence of the genomic shock resulting in numerous chromosomal rearrangements.

RAPID CHANGES IN GENE REGULATION AND GENE SILENCING IN ALLOPOLYPLOIDS

It is now apparent that changes at the sequence level may take place immediately when new allopolyploids are produced [20]. The first example to be reported was that of Song et al. [21] in *Brassica*. Synthetic polyploids were derived, using pure lines, from reciprocal interspecific hybridisation between single plants of the diploid species *B. rapa*, *B nigra* and *B. oleracea*. Colchicine-doubled hybrids were self-pollinated to give F_2 progenies. Further selfed generations were then produced as far as the F_5. RFLP analysis comparing the F_2 with their derived F_5 progenies showed a wide range of changes: most changes involving loss or gain of parental restriction fragments and the appearance of novel fragments in the F_5. It was also shown, using several probes, that RFLP changes could be detected in each generation from the F_2 to the F_5. The frequency of changes varied between the different hybrids used. Detailed cytological analysis was not carried out, so it cannot be ascertained to what extent homeologous recombination accounts for some of these results; and neither was the possible effect of the colchicine treatment considered.

A more convincing study is that of Kashkush et al. [22] in a newly synthesised wheat allopolyploid. The transcriptome response was investigated by analysing 3,072 transcripts in a first generation synthetic bivalent-forming allopolyploid and its two diploid progenitors, *Aegilops sharonensis* and *Triticum monococcum*. cDNA-AFLP band patterns revealed that 60 out of the

3072 transcripts were altered in a reproducible way. Forty-eight transcripts disappeared and 12 were activated. The disappearance of transcripts was due to either gene silencing or gene loss, as confirmed by sequencing. Silencing included genes for RNA, metabolism, disease resistance and cell cycle regulation; and these changes occurred via genetic and epigenetic alterations immediately after the polyploids were formed. Gene loss is an irreversible process, whereas silencing by methylation is epigenetic. The authors conclude that wide hybridisation and/or chromosome doubling triggers a 'genome shock' as proposed by McClintock [23]. Disturbance of genome integrity does not always occur, however, and AFLP analysis in cotton allopolyploids covering *ca* 22,000 genomic loci failed to detect any changes in both allotetraploids and allohexaploids [24].

Epigenetic effects

Changes in cytosine methylation patterns are known to occur frequently within genes and transposable elements in newly formed allopolyploids of *Arabidopsis*, *Brassica* and wheat [21, 25, 26]. The best known example of redundant genes being silenced in an allopolyploid or a diploid hybrid is that of the rRNA genes from one or the other parent at the nucleolar organizer region, *i.e*. nucleolar dominance, reviewed by Pikard [27]. The basis of this phenomenon is not clear, but an attractive recent interpretation is that of Viegas et al. [28] who point out that the dominant parent displaying the NOR in hybrids is the one with the smaller genome, and that explanations can be sought in terms of competition for nuclear space and states of chromatin organisation.

CHROMOSOME ADDITIONS AND SUBSTITUTIONS

The substitution of chromosomes, and of chromosome segments, is used in introgression breeding as a way of transferring traits between related species. Given what we now know about the way that genomes interact in newly made polyploids the question arises as to what extent introgressed pieces of chromatin, or genes, respond to finding themselves in an alien nuclear environment. As yet we have no answers to this question in most cases, except to say that failure to find an introgressed trait will not necessarily mean the failure of introgression of chromatin: it may be a case of chromatin modification or lack of gene expression.

Exceptionally, there are situations where the addition or substitution of chromosomes challenge the integrity of the genome and produce startling and unexpected results, as explained below.

"Cuckoo" chromosomes

The story of "cuckoo" chromosomes is bizarre. Monosomic addition lines (2n = 6x +1 = 43) have been produced following crosses between *Aegilops sharonensis* (2n = 2x = 14) and *Triticum aestivum* (2n = = 6x = 42). In such a situation it is expected that the additional chromosome will be largely eliminated at meiosis and will show low transmission. This is what happens, with the exception of chromosome $4S^1$ which shows preferential transmission and is carried in all of the functional gametes. Meiosis takes place normally for the 42 wheat chromosomes, but thereafter the majority of the gametes which **do not carry** $4S^1$ undergo chromosome fragmentation in the embryo sacs and pollen. The $4S^1$ addition has pollen "killer" genes and it destroys all pollen grains except those within which it is carried, thus ensuring its own preferential transmission into all the viable progeny [29, 30]. Genome integrity is compromised by a 'selfish' chromosome, but the evolutionary significance is difficult to understand – how does such a chromosome come to exist when its selfish manifestation is a human consequence and it does not have such opportunity in nature? In any event it has usefulness in the way that it can be used to cause chromosome breakage and induce translocations between wheat and rye chromosomes in wheat–rye hybrids that have also been constructed to carry the $4S^1$ chromosome.

Supernumerary B chromosomes are common in nature, but rare in crop plants, and whilst they are of general interest in terms of genome integrity [33] they are beyond the scope of this article.

Gene silencing in transgenic plants

Genome integrity is compromised in transgenic plants and can result in gene silencing. The phenomenon is not completely understood, but some mechanisms can be presented [34].

Position effect

Position effect leads to transcriptional gene silencing (TGS) and is associated with heavy methylation of the silenced loci caused by inactive flanking DNA which characterises large parts of the genomes of plants. The methylation spreads to the transgene. It is also thought that some transgenes which are poorly expressed have prokaryotic vector DNA attached to them, and this can prevent binding to nuclear proteins and then trigger methylation. Stable expression is achieved with single un-rearranged copies of a construct that lack any associated vector DNA and are flanked by AT-rich regions that can bind to natural matrix attachments. The problem of TGS is dealt with by regenerating

many independent transformants and then finding those with heritable and stable expression.

Homology-dependent gene silencing

This mode of silencing involves post-transcriptional gene silencing (PTGS) and occurs when there is a homology between interacting genes in the transcribed region. It can occur between a transgene and a homologous endogenous gene (co-suppression), or two homologous transgenes following multiple insertion, and involves the degradation of RNA transcripts. PTGS can be used effectively for the downregulation to deliberately silence genes coding, for example, for allergens and fruit ripening.

ENVIRONMENTAL MODULATION OF REPETITIVE DNA

It has been known since at least the 1960s that genomes have the capacity to be fluid in their integrity in relation to their repetitive DNA elements. Heritable changes in genome organisation in response to environmental stimuli were clearly demonstrated by Durrant and Tyson [35] and Durrant [36], who showed how different combinations of fertiliser treatments in a pure line of flax could induce heritable changes in phenotypes – changing the 'plastic' parent line into large and small 'genotrophs'. Alterations in nuclear DNA amounts and qualities in these genotrophs were confirmed later [37]. Later developments of this story are given in Ceccarelli et al. [38], who report on genome plasticity in *Festuca arundinacea*. These authors grew seeds at temperatures of 10 °C and 30 °C and then analysed the copy number of some repetitive sequences recognised by specific probes. Probes *Fa*H8, *Fa*H13 and *Fa*H14 revealed their target repeats to be more highly represented in seedlings grown at 30 °C than in those grown at 10 °C, and sequences recognised by probe *Fa*A5 were more clearly represented in the genome of seeds grown at the lower temperature. *In situ* hybridisation studies showed the sequences to be scattered along the length of all of the chromosomes. The conclusion is that redundancy modulation of these interspersed repeats allows for direct response of the genome of *F. arundinacea* to changes in temperature. It is not reported if these changes are heritable, but at least it can be said that they are not epigenetic. It is known that the genome size of *F. arundinacea* populations is positively correlated with the mean temperature in the localities where they are grown [38].

CONCLUDING REMARKS

The integrity of genomes reflects their evolutionary history and the way in which their component parts are organised in a balanced and functional way. Human intervention for the purposes of plant improvement can compromise this integrity when different genomes are combined together as allopolyploids, or when whole chromosomes, parts of chromosomes or single genes are introgressed into alien backgrounds. The outcomes from such challenges range from the elimination of whole genomes through to the silencing of individual transgenes, with the result that the new modifications may not correspond in functional terms with the breeder's objectives. On the one hand, the breeding strategy may be undermined, as with gene silencing, while on the other hand advantage may be gained when silencing is used for the downregulation of the expression of undesirable genes. In any event, the way that genomes 'sense' the presence of alien DNA presents us with a problem, as well as with possible advantages. In introgression breeding we may well transfer a chromosome or a chromosome segment from one species into the background of another, but we may not assume that the genes carried on such a segment will be expressed or will be expressed in the desired way.

The interactions between genomes have several aspects. In addition to the nuclear cytoplasmic conflicts, genomes may differ in terms of their repetitive DNAs (a feature on which GISH analysis is based), and this must impact upon the way in which different genomes work together within a common nucleus. Processes of gene regulation may also vary between species, as may the details of chromatin organisation (a poorly understood aspect). Transcription factors may be particularly sensitive to differences in the states of chromatin (protein/DNA interactions). Whatever mechanisms are involved in these nuclear conflicts, natural events then take place to stabilise genome modifications and bring about the coherence which enables gene expression programmes to run.

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I. Pašakinskienė, R. N. Jones

PASIKĖSINIMAS Į GENOMO VIENTISUMĄ

S a n t r a u k a

Selekcininkai siekia išplėsti genetinės įvairovės ribas, kurdami tarprūšinius ir tarpgentinius hibridus, vykdydami introgresinę selekciją ir kurdami transgeninius augalus. Šis kūrybos procesas išklibina prigimtinę branduolio pusiausvyrą. Svetimas genomas arba jo dalis, net atskira pridėtinė chromosoma, pernešta į naują aplinką, ar svetimas genas gali sutrikdyti genomo vientisumą ir branduolyje sukelti genetinį konfliktą. Šių konfliktinių sutrikimų, kaip ir aplinkos streso, pasekmės gali būti įvairios ir sprendžiamos veikiant įvairiems mechanizmas, tokiems kaip: atskiro genomo eliminacija, genomų persitvarkymas alopoliploiduose, staigūs pokyčiai alopoliploidų genų reguliacijoje ir genų nuslopinimas, pridėtinių chromosomų atsiradimas, arba chromosomų substitucija, genų nuslopinimas transgeniniuose augaluose, taip pat kartotinių DNR sekų moduliacijos, sukeltos aplinkos sąlygų. Šiame straipsnyje minėti reiškiniai apžvelgiami per augalų genomo vientisumo prizmę, parodoma, kaip tai galėtų padėti selekcininkams arba, atvirkščiai, kliudyti jų darbui.