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Establishment of a tetraploid cytotype in a diploid population: Effect of relative fitness of the cytotypes

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Abstract

The conditions for the establishment of a tetraploid in a diploid population were investigated by means of a deterministic model, on the assumption that the diploid cytotype produces some *2n* gametes.

If the fertility and viability of both cytotypes were the same and the initial population was diploid, then a mixed population would occur if the production of *2n* gametes was below 17.16%. The tetraploid excluded the diploid above this limit. By modifying the fertility and the viability of the polyploid this threshold varied, dropping to 10% when one of the two parameters was twice that of the diploid, and falling to as low as 6% if both fertility and viability were double that of the diploid.

The conditions for the establishment of a polyploid are therefore quite restrictive under the assumptions of this model. In nature, such processes would probably allow the spread of the polyploid only if the immigration of polyploids considerably enhanced the frequency of tetraploids, or if genetical or environmental changes, or chance processes in small populations caused a substantial increase in the frequency of *2n* gametes produced by the diploid.

Introduction

Polyploidy is a widespread phenomenon in plants. Stebbins (1971, p. 124), by comparing the chromosome numbers of species belonging to the same genera, estimated that 30–35% of the angiosperms are polyploid. Presumably, polyploid species originated as a result of the establishment of polyploid individuals in diploid

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populations. The processes involved, the rate of production of the polyploids and their fate in the diploid population, should therefore be considered in a population perspective. Polyploids may appear in the progeny of diploids by several mechanisms such as polyspermaty, somatic doubling and gametic non-reduction (Grant, 1981, p. 309). Occurrence of *2n* gametes has been reported in many groups of plants. Franke (1975) listed 31 families, and Harlan and deWet (1975) reviewed 84 genera in which they were observed. It is consequently not surprising that *2n* gametes are generally considered to have played an important role in the origin of polyploids in nature (deWet, 1980; Favarger, 1984; Franke, 1975; Gottschalk, 1976, p. 11; Grant, 1981, p. 309; Harlan and deWet, 1975; Jackson, 1976; Lewis, 1980).

The conditions for the success of a new polyploid have been extensively discussed in the context of empirical considerations. These considerations have centered on competition between polyploids and their diploid progenitors, on habitat divergence among the cytotypes, and on the colonizing ability of the polyploid (deWet, 1980; Jackson, 1976). Long life-cycles and vegetative reproduction enhance the chances for the polyploid to persist in spite of reduced fertility (Stebbins, 1971, p. 128–130). The breeding system may influence the chances of establishment of a polyploid. Autogamy lowers the probability of intercytotype matings that may produce hybrids with a low fitness (Jackson, 1976; Stebbins, 1971, p. 130–131). Furthermore, apomixis avoids the problem of meiotic disturbances and helps restore seed production (deWet, 1980).

In comparison to the large number of verbal hypotheses, there have been only two theoretical papers testing the conditions for the coexistence of two cytotypes (Levin, 1975; Fowler and Levin, 1984). In the minority cytotype exclusion model, Levin (1975) assumed that intracytotype pollinations produced viable offspring but intercytotype matings did not. The minority cytotype underwent a higher proportion of ineffective (intercytotype) pollinations than did the majority cytotype. Consequently, seed production was reduced more in the minority cytotype than in the other one and its frequency decreased in subsequent generations, until it became extinct. Fowler and Levin (1984) extended this model by incorporating the Lotka-Volterra competition equations. This extended model also took into account the amount of niche separation, which was assumed to be proportional to the reduction in pollen flow. It was found that the two cytotypes could coexist, one cytotype could replace the other, or the outcome depended on the initial frequencies; but the necessary conditions for the persistence of the polyploid were quite restrictive.

These models took into account the factors influencing the maintenance of polyploids but did not include the processes of their formation. A deterministic model of a population is presented here, in which the diploid cytotype produces some *2n* gametes, and, consequently, some tetraploid offspring appear with each generation. The conditions for establishment of the polyploid are investigated by varying the frequency of *2n* gametes generated by the diploid, and by varying the relative fertility and viability of the cytotypes.

The model

The present model assumes that the diploids produce [u] male and female *2n* gametes and consequently [$1 - u$] haploid ones. The tetraploids produce only diploid gametes. Fertility [f] is assumed to be equal for both male and female functions. The fertility and viability [v] of the tetraploid are expressed relatively to that of the diploid. If the cytotypes have the same generation time, the gametes mate at random and the triploids are lethal, the frequency of the diploids at generation $t + 1$ [d_{t+1}] is a function of the fraction of haploid gametes produced by the diploid and its frequency at generation t [d_t]. Tetraploids may be produced by the fusion of two of their gametes, by the union of one gamete of the tetraploid and one *2n* gamete of the diploid, or by the mating of two *2n* gametes. The recursion equations of the frequency of the diploid [d_{t+1}] and of the tetraploid [t_{t+1}] are then:

$$\begin{aligned} d_{t+1} &= (1-u)^2 d_t^2/k \\ t_{t+1} &= [u^2 d_t^2 + 2ufd_t(1-d_t) + f^2(1-d_t)^2]v/k \\ &= [ud_t + f(1-d_t)]^2 v/k \end{aligned} \qquad [1]$$

where

$$k = (1-u)^2 d_t^2 + \{[ud_t + f(1-d_t)]^2 v\}$$

The equations are weighted by [k] in order to set the sum of the frequencies of the cytotypes in each generation to one.

The equations [1] are used:

i) to study the conditions for coexistence of both cytotypes as a function of the fitness of the tetraploid, when no *2n* gametes are produced by the diploid.

ii) to evaluate the changes in frequency of the cytotypes through time as a function of the fraction of *2n* gametes produced by the diploid, and assuming that both cytotypes have the same fertility and viability.

iii) to determine the effect of fertility and viability of the tetraploid on the conditions of its establishment.

In the first two cases, the equations were solved analytically. Stability analyses were performed by calculating, for the equilibrium point, the absolute value of the derivative of the recursive function (Edelstein-Keshet, 1988, pp. 40–44). In the last case, the solutions were found by simulation because of the complexity of the equations, and stability analyses were solved graphically (Edelstein-Keshet, 1988, pp. 49–51).

Results

i) If the diploid produces no *2n* gametes the recursion equations become:

$$\begin{aligned} d_{t+1} &= d_t^2/k \\ t_{t+1} &= f^2 v(1-d_t)^2/k \\ k &= d_t^2 + f^2 v(1-d_t)^2 \end{aligned}$$

Equilibria were calculated by solving the equation $[d_{t+1} = d_t]$:

$$d = d^2/[d^2 + f^2v(1 - d)^2]$$

Stability analysis shows that a stable equilibrium exists if the population is composed only of diploids or only of tetraploids. An unstable coexistence occurs if the frequency of the diploid is $[f^2v/(f^2v + 1)]$, which depends only on the components of fitness: the relative fertility $[f]$ and viability $[v]$ of the cytotypes. In this latter case, the tetraploid excludes the diploid when the initial frequency of the diploid is below its equilibrium value. Conversely, the polyploid is excluded when the initial frequency of the diploid is higher than its equilibrium value.

The frequencies of the cytotypes at the unstable equilibrium boundaries are shown in Fig. 1 as a function of the product $[f^2v]$, considered to be a measure of the fitness of the tetraploid. As this increases, the frequency of the tetraploid needed for it to become established decreases non-linearly. However, even for high fitnesses of the tetraploid cytotype, a substantial initial frequency is necessary for its establishment.

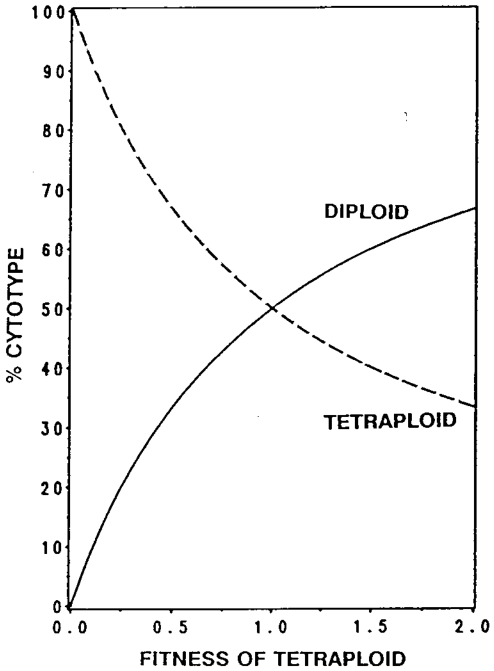

Fig. 1. Frequencies of the cytotypes at the unstable equilibrium boundaries when the diploid produces no *2n* gametes. The frequencies are expressed as a function of the fitness of the tetraploid, defined as the product of the square of its fertility and its viability.

ii) If the diploid cytotype produces a given level of *2n* gametes and if both cytotypes have the same fitness, the recursion equations become:

$$d_{t+1} = (1-u)^2 d_t^2 / k$$
$$t_{t+1} = [1-(1-u)d_t]^2 / k$$
$$k = (1-u)^2 d_t^2 + [1-(1-u)d_t]^2$$

The conditions of coexistence of both cytotypes at equilibrium are determined by the following equation:

$$d[2(1-u)^2 d^2 - (u^2 - 4u + 3)d + 1] = 0$$

It has 3 solutions:

$$[\mathrm{a}]\ d = 0$$
$$[\mathrm{b}]\ d = \frac{3 - u - \sqrt{u^2 - 6u + 1}}{4(1-u)}$$
$$[c]\ d = \frac{3 - u + \sqrt{u^2 - 6u + 1}}{4(1-u)}$$

Equilibrium [a] is stable. Equilibria [b] and [c] have real values only if $[u^2 - 6u + 1 > 0]$, which is realized when $[u < 0.1716]$. Under this condition, [b] is an unstable and [c] is a stable equilibrium. On the graph of $[d_{t+1} = f(d_t)]$ (Fig. 2), the equilibria points correspond graphically to the intercepts of the bisecting line with the function. The evolution of two populations, one with an initial proportion of diploid below the unstable equilibrium [b], and the other above it, is illustrated according to the "cobwebbing method" (Edelstein-Keshet, 1988, pp. 49–50). If the initial proportion of diploid in the population is below [b], then the diploid is excluded. If it is above this value, then a stable coexistence occurs in [c].

When both cytotypes coexist in a population at equilibrium [c], a change in the frequency of the diploid allows the establishment of the tetraploid if the frequency of the diploid drops below the unstable equilibrium value [b]. Table 1 illustrates the values of equilibria [b] and [c] for several frequencies of *2n* gametes. The difference between the two values decreases as the frequency of *2n* gametes increases. Consequently the production of *2n* gametes reduces the decrease of diploid necessary for the establishment of the tetraploid.

For $[u > 0.1716]$, the diploid is excluded and the tetraploid becomes established. This point is illustrated in Fig. 3 in which the evolution of an initially diploid population is shown for several frequencies of *2n* gametes.

iii) The conditions of coexistence of the cytotypes were also analyzed when the cytotypes did not have the same fertility and viability. The equilibrium equation is:

$$d\{[(1-u)^2 + (f-u)^2 v)]d^2 - [(1-u)^2 + 2(f^2 v - fvu)]d + f^2 v\} = 0$$

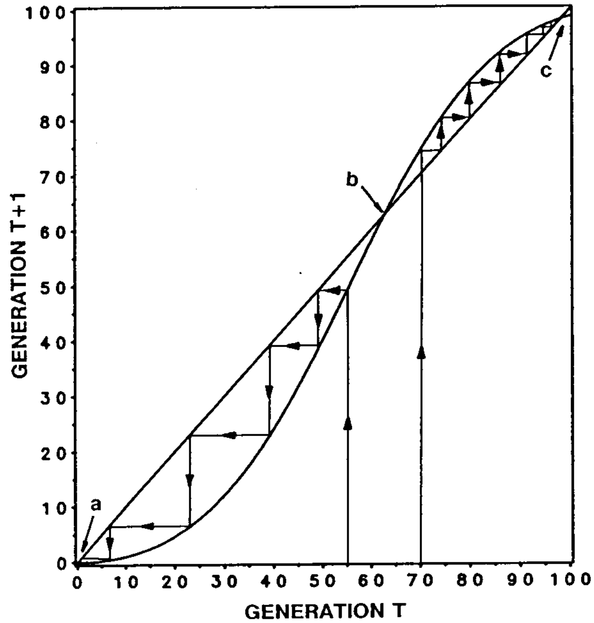

Fig. 2. Frequency of diploids at generation [$t + 1$], as a function of its frequency at generation [t], when the diploid produces 10% of $2n$ gametes and both cytotypes have equal fitness. The intersections of the function with the bisecting line defines the equilibria points [a, b, and c]. Equilibria [a] and [c] are stable. Equilibrium [b] is unstable. The evolutions of two populations, one with an initial frequency of diploids below the unstable equilibrium point, and the other above it, are drawn.

Its solutions are:

[a] $d = 0$

[b] $$d = \frac{(1-u)^2 + 2(f^2v - fvu) - \sqrt{X}}{2[(1-u)^2 + (f-u)^2v]}$$

[c] $$d = \frac{(1-u)^2 + 2(f^2v - fvu) + \sqrt{X}}{2[(1-u)^2 + (f-u)^2v]}$$

where

$$X = u^4 - 4(1 + fv)u^3 + 2(3 + 4fv)u^2 - 4(1 + fv)u + 1$$

As in the previous case, equilibrium [a] is stable. Equilibria [b] and [c] have real values only if [$X > 0$]. [b] is an unstable and [c] is a stable equilibrium under this condition. As in case [ii], the diploid is excluded if its initial frequency in the population is below [b] and a stable coexistence occurs in [c] if its initial frequency is above [b]. If [$X < 0$], then the tetraploid becomes established. Fertility and viability appear only as the product [fv] in the square root of equilibria [b] and [c]. Consequently these parameters have identical effects on the threshold of exclusion of the diploid. However, the [f^2v] terms in equation [c] and [d] imply that fertility

Table 1. Frequency of the diploid cytotype at the unstable equilibrium, at the higher stable equilibrium, and difference between the equilibria as a function of the frequencies of *2n* gametes if the cytotypes have equal fitness. The values are expressed as a percentage.

frequency of *2n* gametes	unstable equilibrium	higher stable equilibrium	difference
0	50	100	50
1	51	100	49
2	52	100	48
3	53	100	47
4	54	100	46
5	56	100	44
6	57	100	43
7	58	99	41
8	60	99	39
9	61	99	38
10	63	98	35
11	65	98	33
12	66	97	31
13	68	96	28
14	71	95	24
15	74	94	20
16	77	92	15
17	82	88	6

and viability will not have equal effects on the equilibrium proportions of the cytotypes when they coexist.

In the case of an initially diploid population, the frequencies of the cytotypes when stable coexistence occurs (equilibrium [c]), and the threshold of exclusion of the diploid, were determined by simulation assuming that either fertility or viability varies, the other parameter being equal for both cytotypes. The frequency of the tetraploid maintained in the population as a function of the proportion of *2n* gametes produced by the diploid is shown for several relative fertilities and relative viabilities of the tetraploid in Fig. 4 and Fig. 5 respectively. In both cases the diploid and the tetraploid coexist for low frequencies of *2n* gametes. Even if the fertility of the polyploid is zero, it is maintained in the population because it is produced continuously in the population. The frequency of *2n* gametes necessary for exclusion of the diploid decreases as the fertility or viability of the tetraploid increases. For example, the diploid is excluded when *2n* gametes are more frequent than 10% if fertility or viability of the tetraploid is twice that of the diploid. If one of these is four times greater, the diploid is excluded when the frequency of *2n* gametes is above 5.5%. Even if the tetraploid has a lower fitness than the diploid, the tetraploid can exclude the diploid if the diploid produces a substantial proportion of *2n* gametes.

When both fertility and viability are increased, then the level of *2n* gametes leading to the establishment of the polyploid decreases, as shown in Table 2. Table 2 is symmetrical about its diagonal, because fertility and viability are reversible in the square root of the stable equilibrium [c].

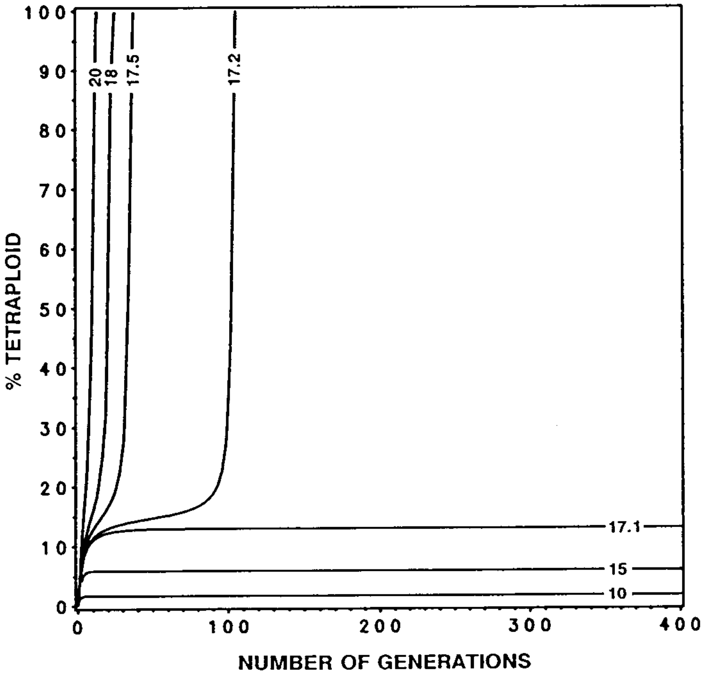

Fig. 3. Change of the frequency of the tetraploid for several levels of *2n* gametes (as a percentage), as a function of the number of generations. The initial population is diploid and the cytotypes have equal fitness.

Table 2. Threshold of *2n* gametes produced by the diploid determining the fixation of the tetraploid, as a function of its fertility and its viability relative to that of the diploid. The values are expressed as a percentage of *2n* gametes, and rounded to the nearest whole value.

Fertility	Viability									
	0.2	0.4	0.6	0.8	1.0	1.2	1.4	1.6	1.8	2.0
0.2	67	57	51	46	42	38	36	34	32	30
0.4	57	46	38	34	30	27	25	23	21	20
0.6	51	38	32	27	24	21	19	18	16	15
0.8	46	34	27	23	20	18	16	14	13	12
1.0	42	30	24	20	17	15	13	12	11	10
1.2	38	27	21	18	15	13	12	10	9	8
1.4	36	25	19	16	13	12	10	9	8	8
1.6	34	23	18	14	12	10	9	8	7	7
1.8	32	21	16	13	11	9	8	7	6	6
2.0	30	20	15	12	10	8	8	7	6	6

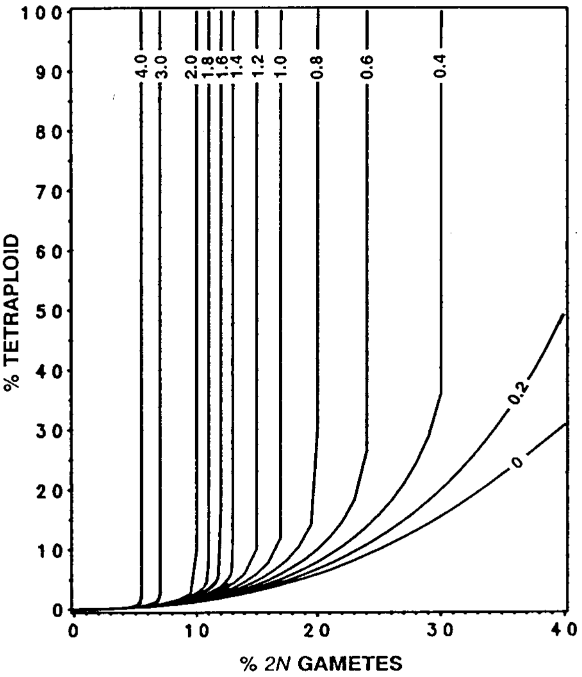

Fig. 4. Frequency at equilibrium of the tetraploid cytotype for different values of its fertility relative to that of the diploid, and as a function of the frequency of *2n* gametes produced by the diploid cytotype. The cytotypes have equal viability.

Discussion

The conditions for equilibrium determined here may be compared to the minority cytotype exclusion model (Levin, 1975). When the diploid produces no *2n* gametes and the cytotypes have the same fitness, both models show that an unstable equilibrium exists when there is 50% of each cytotype. Although intercytotype pollination has not been taken into account explicitly in the present model, triploids are assumed to be sterile or lethal. Therefore, the less frequent cytotype suffers minority disadvantage.

Consequently it may appear that minority cytotypes will always be excluded. However, the present model shows that a higher fitness of one cytotype may partly compensate for the minority disadvantage. Moreover, when the production of *2n* gametes is taken into account, a low frequency of polyploids can be maintained in the population, even below the critical threshold where the polyploid would spread to fixation, and even if the starting population is diploid. This result is in agreement with the observation that most large sexual plant populations include at least some polyploid individuals (Böcher, 1961; Darlington, 1963, p. 54; Löve, 1964).

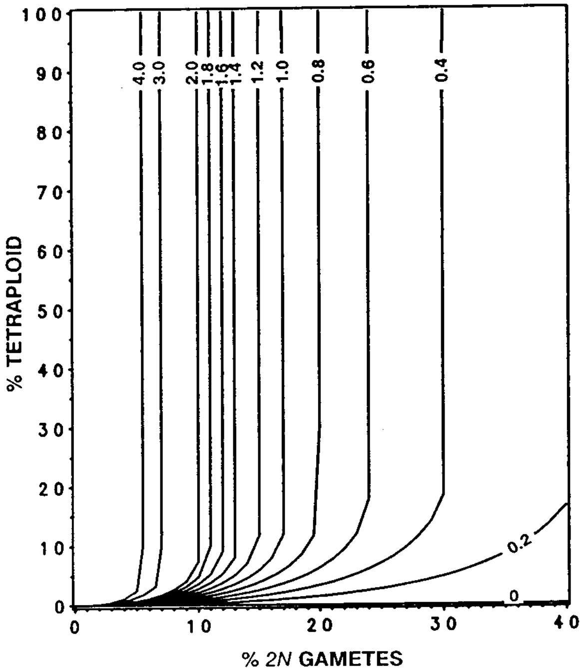

Fig. 5. Frequency at equilibrium of the tetraploid cytotype for different values of its viability relative to that of the diploid, and as a function of the frequency of *2n* gametes produced by the diploid cytotype. The cytotypes have equal fertility.

Although *2n* gametes can maintain polyploids at a low frequency in the population, it is also clear that the establishment of a new polyploid in a diploid population is possible only if the diploid cytotype produces a rather high frequency of *2n* gametes. There is a lack of field data on the occurrence of *2n* gametes in natural populations. Nevertheless, a large number of factors have been shown to influence their production.

Genetic determination of *2n* gamete formation is known in a few species. In *Datura* (Satina and Blakeslee, 1935), maize (Rhoades and Dempsey, 1966), and alfalfa (McCoy, 1982), a single recessive gene is responsible for the formation of *2n* male or female gametes. In potato, Mok and Peloquin (1975) found three meiotic mechanisms of *2n* pollen formation, and suggested that each one was controlled by a single recessive gene. Subsequently, alternative hypotheses were proposed, such as the presence of both major and minor genes (Jacobsen, 1980), or of an incompletely penetrant gene with variable expressivity (Veilleux and Lauer, 1981).

Environmental conditions influence the production of *2n* gametes. For example, McHale (1983) regularly observed a high production of *2n* pollen in clones of *Solanum phureja* cultivated in a coastal field which provided uniformly cool growing conditions (means of 76% and 80% during two successive years, up to 98% for one clone). In contrast, the same clones cultivated in an inland greenhouse with warmer and more fluctuating temperatures produces on average 35% and 27% *2n* pollen during the two years. Low and high temperatures have been shown to induce the production of *2n* gametes (reviewed by Stein, 1970), as well as a cold treatment followed by a warm one (Sax, 1937). Quantitative estimations of the effects of temperature have been given by McCoy (1982) who grew clones of diploid alfalfa either in a greenhouse (25° C $\pm$ 5° C) or in growth chambers (25° C constant or 30° C day/10° C night) under the same light regime (16 h. day/8 h. night). Variations in the production of *2n* gametes occurred within environments (range of 4% to 37% in one clone) and between environments (range of 7% to 50% in one clone). No environment resulted systematically in a high *2n* pollen production in all clones.

Other factors, such as dehydration (Gilles, 1939) or low nutrients, may favor the production of *2n* gametes (Grant, 1952). Grant (1952) observed that diploid F1 hybrids of *Gilia* produced over 800 times the number of viable tetraploid progeny when cultivated in sand, than when grown on fertilized soil. Parasites such as mites (Kostoff and Kendall, 1929) or viruses (Swaminathan et al., 1959; Sandfaer, 1973) may induce meiotic aberrations which occasionally lead to the formation of *2n* gametes. For example, healthy varieties of diploid barley spontaneously produced between 0 and 0.29% triploids (Sandfaer, 1975) but as many as 3.8% when infected by a virus (Sandfaer, 1973).

Most of these data were collected on cultivated plants, and indeed often on plants previously selected for their high production of *2n* gametes. Nevertheless, transposing these results to natural populations implies that a diploid population may maintain a low level of *2n* gametes for a long time, but mutations, environmental changes or parasites may induce a considerable increase in their production. This increase may then allow the tetraploid to spread to fixation. In small populations, the magnitude of these processes leading to *2n* gametes formation at times will be accentuated as a result of chance effects, and this may further enhance the likelihood that tetraploids will go to fixation (Fowler and Levin, 1984). Moreover, a fall in the frequency of the diploid cytotype may occur in a finite population by immigration of tetraploid individuals. In this case also, *2n* gametes promote the establishment of the polyploid cytotype by lowering the decrease of diploid necessary for fixation of the tetraploid.

The present study provides a quantitative estimate of the effect of fitness of the tetraploid on its chances of establishment when *2n* gametes are produced by the diploid. A review of the literature also shows that the production of *2n* gametes should not be considered to be always low and therefore unimportant, but that such production can vary substantially and consequently influence the chances of establishment of the polyploid. Furthermore, the production of *2n* gametes is not only a factor promoting polyploidy but has also been considered to be an important process by which polyploids arise in nature (deWet, 1980; Favarger, 1984; Franke, 1975; Gottschalk, 1976, p. 11; Grant, 1981, p. 309; Harlan and deWet, 1975; Jackson, 1976; Lewis, 1980). It is consequently an essential parameter to introduce into theoretical considerations of the establishment of polyploids in a diploid population. It is a necessary complement to studies such as those of Levin (1975) and Fowler and Levin (1984), focusing on the future of a mixed population.

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References

Böcher, T. W. 1961. The development of cytotaxonomy since Darwin's time. pp. 26–43. *In* P. J. Wanstall (ed.). A Darwin centenary. Botanical Society of the British Isles, London.

Darlington, C. D. 1963. Chromosome botany and the origins of cultivated plants. Hafner, New York.

deWet, J. M. J. 1980. Origins of polyploids. pp. 3–15. *In* W. H. Lewis (ed.). Polyploidy – Biological relevance. Plenum, New York.

Edelstein-Keshet L. 1988. Mathematical models in Biology. Random House, New York.

Favarger, C. 1984. Cytogeography and biosystematics. pp. 453–476. *In* W. F. Grant (ed.). Plant biosystematics, Academic Press, Toronto, New York.

Fowler, N. L., and D. A. Levin. 1984. Ecological constraints on the establishment of a novel polyploid in competition with its diploid progenitor. Am. Nat. 124: 703–711.

Franke, R. 1975. Ueber das Auftreten von unreduzierten Gameten bei Angiospermen. Arch. Züchtungforsch. 5: 201–208.

Gilles, N. 1939. The effect of dehydration on microsporogenesis in *Tradescantia.* Amer. J. Bot. 26: 334–339.

Gottschalk, W. 1976. Die Bedeutung der Polyploidie für die Evolution der Pflanzen, Gustav-Fischer, Stuttgart.

Grant, V. 1952. Cytogenetics of the hybrid *Gilia millefoliata* X *achilleaefolia.* I. Variations in meiosis and polyploidy rate as affected by nutritional and genetic conditions. Chromosoma 5: 372–390.

Grant, V. 1981. Plant speciation. Second edition. Columbia University Press, New York.

Harlan, J. R., and J. M. J. deWet. 1975. On Ö. Winge and a prayer: the origins of polyploidy. Bot. Rev. 41: 361–390.

Jackson, R. C. 1976. Evolution and systematic significance of polyploidy. Ann. Rev. Ecol. Syst. 7: 209–234.

Jacobsen, E. 1980. Increase of diplandroid formation and seed set in 4x × 2x-crosses in potatoes by genetical manipulation of dihaploids and some theoretical consequences. Z. Pflanzenzüchtg. 85: 110–121.

Kostoff, D., and J. Kendall. 1929. Irregular meiosis in *Lycium halimifolium* Mill. produced by gall mites (Eriophyes). J. Genet. 21: 113–115.

Levin, D. A. 1975. Minority cytotype exclusion in local plant populations. Taxon 24: 35–43.

Lewis, W. H. 1980. Polyploidy in species populations. pp. 103–144. W. H. Lewis (ed.). Polyploidy – Biological relevance. Plenum, New York.

Löve, A. 1964. The biological species concept and its evolutionary structure. Taxon 13: 33–45.

McCoy, T. J. 1982. The inheritance of *2n* pollen formation in diploid alfalfa *Medicago sativa.* Can. J. Genet. Cytol. 24: 315–323.

McHale, N. A. 1983. Environmental induction of high frequency *2n* pollen formation in diploid *Solanum.* Can. J. Genet. Cytol. 25: 609–615.

Mok, D. W. S., and S. J. Peloquin. 1975. The inheritance of three mechanisms of diplandroid (*2n* pollen) formation in diploid potatoes. Heredity 35: 295–302.

Rhoades, M. M., and E. Dempsey. 1966. Induction of chromosome doubling at meiosis by the elongate gene in maize. Genetics 54: 505–522.

Sandfaer, J. 1973. Barley stripe mosaic virus and the frequency of triploids and aneuploids in barley. Genetics 73: 597–603.

Sandfaer, J. 1975. The occurrence of spontaneous triploids in different barley varieties. Hereditas 80: 149–153.

Satina, S., and A. F. Blakeslee. 1935. Cytological effects of a gene in *Datura* which causes dyad formation in sporogenesis. Bot. Gaz. 96: 521–532.

Sax, K. 1937. Effects of variations in temperature on nuclear and cell division in *Tradescantia.* Amer. J. Bot. 24: 218–225.

Stebbins, G. L. 1971. Chromosomal evolution in higher plants. Addison-Wesley. Reading, Mass.

Stein, M. 1970. Polyploidie und Umwelt. Tag.-Ber. Dt. Akad. Landwirtsch.-Wiss., Berlin, 101: 51–68.

Swaminathan, M. S., T. Ninan, and M. L. Magoon. 1959. Effects of virus infection on microsporogenesis and seed fertility in *Capsicum.* Genetica 30: 63–69.

Veilleux R. E. and F. I. Lauer. 1981. Variation for *2n* pollen production in clones of *Solanum phureja* Juz. and Buk. Theor. Appl. Genet. 59: 95–100.