Effect of triploid fitness on the coexistence of diploids and tetraploids

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The conditions for the coexistence of diploids, triploids and tetraploids in a single population were investigated with a deterministic model under the assumptions that diploids might produce $2n$ gametes, and that triploids had a lower fitness than other cytotypes and generated equal proportions of haploid and diploid gametes. When diploids produced only haploid gametes, the dynamics of the cytotypes were similar to that of heterozygote disadvantage with two alleles at a single locus, with triploids being equivalent to the heterozygotes. Production of $2n$ gametes by diploids increased the pool of diploid gametes and created a stable equilibrium involving a majority of diploids and a minority of polyploids. When the fitness of tetraploids was equal to or higher than that of diploids, increased triploid fitness decreased the threshold of $2n$ gametes necessary to deterministically fix tetraploids in the population. Conversely, when tetraploids were less fit than diploids, the rate of $2n$ gamete production leading to the exclusion of diploids first decreases and then increased with increasing triploid fitness. Triploids are repeatedly found in diploid-tetraploid hybridizations and are rarely totally sterile. They might play a determinant role in the future of multiple cytotype populations. The effect of triploids depends on the relative fitness of diploids and tetraploids and is also a function of their fitness.

ADDITIONAL KEY WORDS: population genetics – theoretical model – polyploidy – triploid – $2n$ gametes.

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INTRODUCTION

Most theoretical development of population genetics has assumed Mendelian inheritance among haploid or diploid individuals. While diploidy is predominant among vertebrates, with noteworthy exceptions in amphibians, reptiles and fishes (Sexton, 1980), plants commonly exhibit more complex genetic systems and are often polyploid, or have polyploid populations (Stebbins, 1971: 124; Grant, 1981). The frequency of polyploidy in plant taxa provides ample evidence of the historical importance of polyploidization. However, polyploidization is also an active process with some polyploid individuals frequently being found in most large sexual plant populations (Böcher, 1961; Darlington, 1963; Löve, 1964). Moreover, many populations include a mixture of diploid and polyploid individuals which might arise either by primary intergradation (Urbanska-Worytkiewicz & Landolt, 1978; Vuille, 1986) or more probably following secondary contact (Zohary & Nur, 1959; Lord & Richards, 1977; Felber & Girard, 1986; Lumaret *et al.*, 1987; Van Dijk, Hartog & Van Delden, 1992; Felber-Girard *et al.*, 1996). Yet, at present our understanding of the process of polyploidization is incomplete (Bever & Felber, 1992).

Little theoretical work has been done on populations with multiple ploidy levels. Assuming lethality of triploids, Levin (1975) demonstrated that mixed diploid-tetraploid populations are not stable, with the frequency of the minority cytotype decreasing because it is less likely to engage in fertile intraploidy matings than the majority one. Extending this model to include competition and preferential matings within ploidy in proportion to their niche separation, Fowler & Levin (1984) found limited conditions allowing coexistence of the two ploidy levels. Van Dijk & Bijlsma (1994) have recently demonstrated that reproductive isolation by flowering time alone may be sufficient to allow the coexistence of the two cytotypes.

The three previous models assumed that diploid zygotes only produce haploid (reduced) gametes. While this is indeed the case for regular meiosis, meiotic irregularities may lead to the formation of gametes with a somatic chromosome number ($2n$ gametes) (cf. Veilleux, 1985; Bretagnolle & Thompson, 1995, for review). Tetraploids may arise in diploid-diploid crosses by bilateral sexual polyploidization, i.e. the fusion of two $2n$ gametes (Mendiburu & Peloquin, 1977; Parrott, Smith & Smith, 1985; Werner & Peloquin, 1991) and this process is considered to be an important mode of formation of novel polyploids (Harlan & deWet, 1975; Jackson, 1976; Thompson & Lumaret, 1992). Felber (1991) demonstrated that $2n$ gamete production can exert a strong influence on the dynamics of mixed diploid-tetraploid populations. Tetraploids were maintained in a predominantly diploid population when the rate of diploid production of $2n$ gametes was low. However, when the rate of $2n$ gamete production exceeded a critical point, tetraploids excluded diploids. That threshold corresponded to 17.16% when the two cytotypes had equal fitness, but decreased to 10% if the fertility or viability of the tetraploid was double that of the diploid and even 6% when both were double.

All previously published models of polyploid establishment assume that triploids have negligible fitness. Indeed triploids usually have reduced fertility. Moreover, hybridizations between diploids and tetraploids often yield a lower frequency of triploids than expected because of the low fertility of the crosses, with the strength of this 'triploid block' (*sensu* Marks, 1966) varying between species. While triploid block can be strong, as in *Solanum* (Werner & Peloquin, 1991), *Trifolium pratense* (Taylor & Wiseman, 1988) and in *Lotus tenuis* (Negri & Veronesi, 1989), it is never absolute.

Evidence of lower triploid block is given by the frequent discovery of triploids in contact zones between diploids and tetraploids (Müntzig, 1937; Zohary & Nur, 1959; Lord & Richards, 1977; Felber & Girard, 1986; Felber, in prep.) and in experimental crosses (Jones & Borrill, 1962; Alexander & Beckett, 1963; Van Dijk, Stegeman & Van Delden, 1991b; Van Santen, Hugessen & Casler, 1991; de Haan *et al.*, 1992; Maceira *et al.*, 1992; Needham & Erickson, 1992; Felber, in prep.). Triploids may also arise by the fusion of a reduced gamete and a 2*n* gamete (Rhoades, 1936). Triploids may be partially fertile and act as a transition between two ploidy levels (triploid bridge). Diploids were found in the progeny of triploids backcrossed to diploids in wheat (Vardi, 1974), barley (Pickering *et al.*, 1994), *Dactylis glomerata* (Jones & Borrill, 1962) and *Trifolium pratense* (Taylor & Chen, 1988). Reciprocally, triploids backcrossed with tetraploids yielded tetraploid offsprings in wheat (Vardi & Zohary, 1967; Gerechter *et al.*, 1971; Vardi, 1971), *D. glomerata* (Jones & Borrill, 1962) and *T. pratense* (Taylor & Chen, 1988).

Tetraploids may thus arise from diploids in two ways, directly by the fusion of 2*n* gametes or with the intermediary of a triploid bridge. However, the interaction of these two processes has not been previously analysed theoretically. In this paper, we develop models of the genetics of a single population composed of diploid, triploid, and tetraploid individuals. We use a traditional population genetics framework to explore the interaction of non-zero triploid fitness and gametic non-disjunction in influencing the coexistence of cytotypes, in general, and the establishment of polyploids, in particular.

THE MODEL

The basic model of a polyploid complex

The dynamics of polyploid complexes are principally characterized by the low fitness of triploid individuals as a result of meiotic irregularities. The role of triploids in the dynamics of polyploid complexes depends on the type of gametes that they produce. The gametes composed either of one or two sets of chromosomes will be functional. Those with incomplete chromosome sets or additional chromosomes will have a reduced fitness or will be non-viable. Backcross experiments prove that triploids produce partly haploid and diploid gametes. Therefore, we assume in the present model that triploids produce equal proportions of haploid and diploid gametes.

Assuming that triploids produce equal proportions of haploid and diploid gametes, the dynamics are similar to that of heterozygote disadvantage (underdominance) at a single locus (Haldane, 1942; Li, 1955) with triploids being the heterozygotes. The dynamics of this system can be described by setting the fitness of diploids (W_d), triploids (W_{tr}), and tetraploids (W_t) equal to 1, 1–s, and 1 + t, respectively, with $s + t > 0$. Assuming random union of gametes, regardless of ploidy, we can describe the change in frequency of haploid gametes (r) due to selection as:

$$\Delta r_{sel} = [r(1-r)(s(2r-1)-t(1-r))]/W, \tag{1}$$

where $W = 1-2sr(1-r) + t(1-r)^2$.

According to the classical model of underdominance, this system has two stable equilibria at $\hat{r} = 0$, $\hat{r} = 1$ and an intermediary unstable equilibrium at:

$$\hat{r} = (s + t)/(2s + t) \text{ (Fig. 1A).}$$

Intermediate frequencies of haploid gametes and hence mixtures of ploidy levels are thus unstable, as first described by Levin (1975) for the coexistence of two cytotypes.

If the tetraploid has an equal fitness to that of the diploid, then the equilibrium is independent of triploid fitness and equal to 0.5. Initial frequencies of haploid gametes higher than the equilibrium value will lead to the fixation of the haploid gametes (diploids). Reversely, lower frequencies than the equilibrium value will lead to the fixation of the diploid gametes (tetraploids).

A lower fitness of the tetraploid compared to that of the diploid reduces the equilibrium value and thus favours the establishment of haploid gametes (diploid cytotype). Conversely, a higher fitness of the tetraploid increases the equilibrium value and favours the establishment of the diploid gametes (tetraploid cytotype) (Felber, 1991). When considering the effect of increasing fitness of triploids with a constant tetraploid fitness, the unstable equilibrium, $\hat{r}$, moves further from the value of 0.5, and the rate of change away from this equilibrium decreases. Thus, increasing triploid fitness affects the equilibrium by enhancing the trends caused by changing tetraploid fitness. A higher fitness of triploids will increase the value of the equilibrium for tetraploid fitnesses higher than that of diploids and increase the range

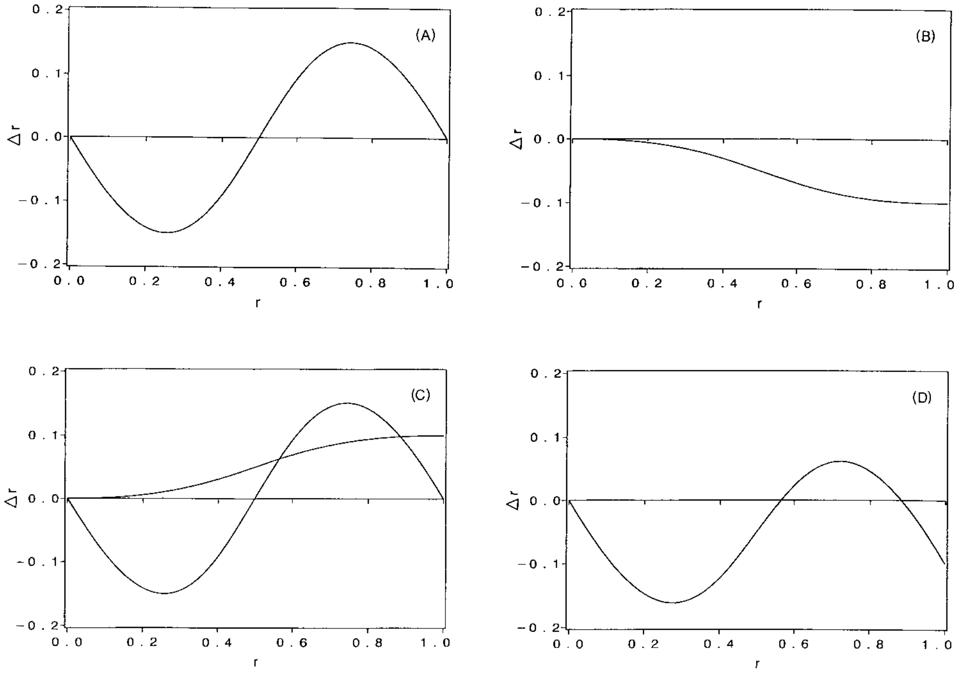

Figure 1. Graphical illustration of the identification of the equilibrium values of the equation for the rate of change in the frequency of the haploid gamete (Δr) assuming that $s = 1$ and $t = 0$. The rate of change of the haploid gamete due to selection against the triploids with respect to the frequency of the haploid gamete, r, is plotted in (A). The rate of change due to the production of $2n$ gametes ($u = 0.1$) in diploid adults is plotted in (B). When the negative of the rate of change due to $2n$ gamete production (1b) is plotted with the rate of change due to selection (1a) as in (C), the curves intersect at the equilibria, as demonstrated in (D). If the frequency of the haploid gametes is initially greater than 0.565, then the population will approach the stable equilibrium of $\hat{r} = 0.885$. If the frequency of haploid gametes in a population is initially less than 0.565 then the population will proceed deterministically to fixation of the tetraploids.

of frequencies of diploid gametes leading to the exclusion of the diploid by the tetraploid. Similarly, it will decrease the equilibrium value for lower tetraploid fitnesses and diminish the range of frequencies of diploid gametes leading to the establishment of the tetraploid.

Diploid 2n *gamete production without fitness reduction*

Continuing with the analogy of this system to that of simple allelic underdominance, 2*n* gamete production in diploids can be likened to mutation with a major difference being that while mutation can occur in any gene regardless of the genotype, 2*n* gamete production only occurs in one of them, the diploids. We can include the effect of a given proportion of 2*n* gamete production in diploids, u, on the rate of change in r as follows:

$$\Delta r_{\text{sel and } 2n \text{ gametes}} = [r(1-r)\ (s(2r-1)-t(1-r))-ur^2]/W, \qquad (2)$$

where W is as in equation 1.

Diploid production of 2*n* gametes alone will cause the frequency of haploid gametes to decrease (Fig. 1B). Note that as a result of 2*n* gamete production only occurring in diploids, the effect of 2*n* gamete production on the equilibria depends on zygotic selection while this would not be the case for an analogous description of the effect of mutation. In fact, strong selection against triploids increases the effect due to 2*n* gametes.

As previously, the three equilibria determined by equation (2) are:

$$\text{(a)}\ \hat{r} = 0$$

$$\text{(b)}\ \hat{r} = \frac{3s+2t-u+\sqrt{s^2-6su-4ut+u^2}}{2(2s+t)}$$

$$\text{(c)}\ \hat{r} = \frac{3s+2t-u-\sqrt{s^2-6su-4ut+u^2}}{2(2s+t)}$$

where $s^2-6su-4ut + u^2 > 0$

(a) and (b) are stable while (c) is unstable (Fig. 1C, D). If triploid fitness is null, and tetraploids have an equal fitness to that of the diploid, then the equilibria (b) and (c) reduce to:

$$\hat{r} = \frac{3-u \pm \sqrt{u^2-6u+1}}{4}$$

The dependence of the two non-trivial equilibria on the rate of 2*n* gamete production in diploids is plotted in Figure 2. As a general pattern, the unstable equilibrium values correspond to lower frequencies of haploid gametes than the peak (left of the peak), while the stable equilibrium have higher values than the peak (right of the peak). The stable equilibrium will be reached when the initial frequencies of haploid gametes are higher than the unstable value and the rate of production of 2*n* gametes is lower than the peak. Points located outside that zone correspond to the establishment of diploid gametes.

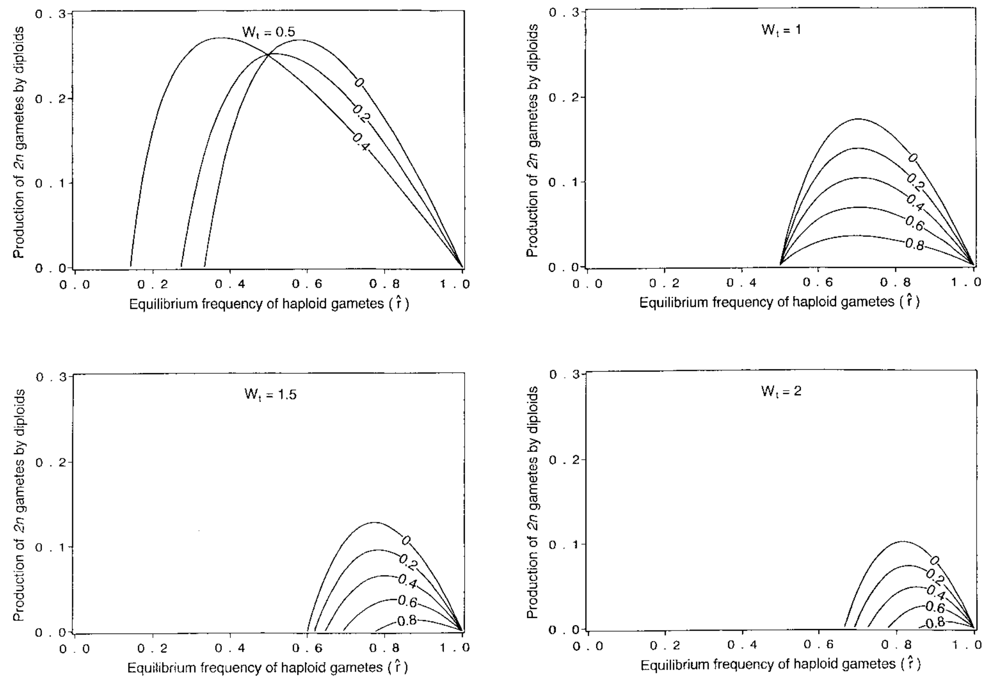

Figure 2. Dependence of the two non trivial equilibria on the rate of $2n$ gametes production for several triploid and tetraploid fitnesses. The fitness of triploids is written on the curves. W_t is the fitness of the tetraploid.

When the tetraploid is less fit than the diploid, then the curves intersect at the same point (Fig. 2, $W_t = 0.5$). For a given level of $2n$ gametes, the unstable equilibrium values decrease as triploid fitness increases. Consequently, increasing triploid fitness increases the range of values for which both cytotypes coexist and consequently decreases that of the establishment of the tetraploids. The rate of production of $2n$ gametes by diploids leading to the exclusion of haploid gametes first decreases and then increases, with increasing triploid fitness. Thus, it is lower for $W_{tr} = 0.2$ than for $W_{tr} = 0$ and $W_{tr} = 0.4$.

If tetraploid fitness equals or is higher than that of the diploid, the curves do not intersect (Fig. 2, $W_t = 1$, 1.5 and 2). Increasing fitness of the tetraploid cytotype enhances the range of values for which the tetraploid gets established. In this case, increasing triploid fitness increases the value of the unstable equilibrium for a given level of diploid $2n$ gamete production. Furthermore, the rate of production of $2n$ gametes necessary for deterministic exclusion of the haploid gametes decreases with increasing triploid fitness as indicated by the lower peaks of the isoclines in Figure 2 for $W_t = 1$, 1.5 and 2. Thus, increasing triploid fitness increases the range of values for which the tetraploid gets established, when tetraploid fitness is higher than diploid fitness.

Diploid 2n *gamete production with fitness reduction*

Note that when a diploid zygote produces a single diploid gamete, it may decrease its production of haploid gametes by two. This would decrease the rate of change of haploid gametes by decreasing the net fitness of diploid zygotes. The resulting equation for the rate of change of haploid gametes is as follows:

$$\Delta r_{\text{sel and nred}} = [r(1-r)(s(2r-1)-t(1-r))-u'r^2(2-r)]/W, \qquad (3)$$

where $W = 1\text{-}2sr(1\text{-}r) + t(1\text{-}r)^2\text{-}u'r^2$ and where u' equals the frequency of the process of 2*n* gamete production and this process reduces the net production of gametes from diploid zygotes by a proportion of u'. Hence, u of equation 2 equals u'/(1-u').

The three equilibria become:

$$\text{(a)}\ \hat{r} = 0$$

$$\text{(b)}\ \hat{r} = \frac{3s + 2t - 2u' + \sqrt{s^2 + 4u'^2 - 8su' - 4u't + 12t(1-s)}}{2(2s + t - u')}$$

$$\text{(c)}\ \hat{r} = \frac{3s + 2t - 2u' - \sqrt{s^2 + 4u'^2 - 8su' - 4u't + 12t(1-s)}}{2(2s + t - u')}$$

(a) and (b) are stable while (c) is unstable.

Discounting of diploid fitness as a result of 2*n* gamete production does not change the general results of the model. However, it does magnify the consequences of 2*n* gamete production, with the magnitude of change of the equilibria being dependent upon the particular conditions (Fig. 3).

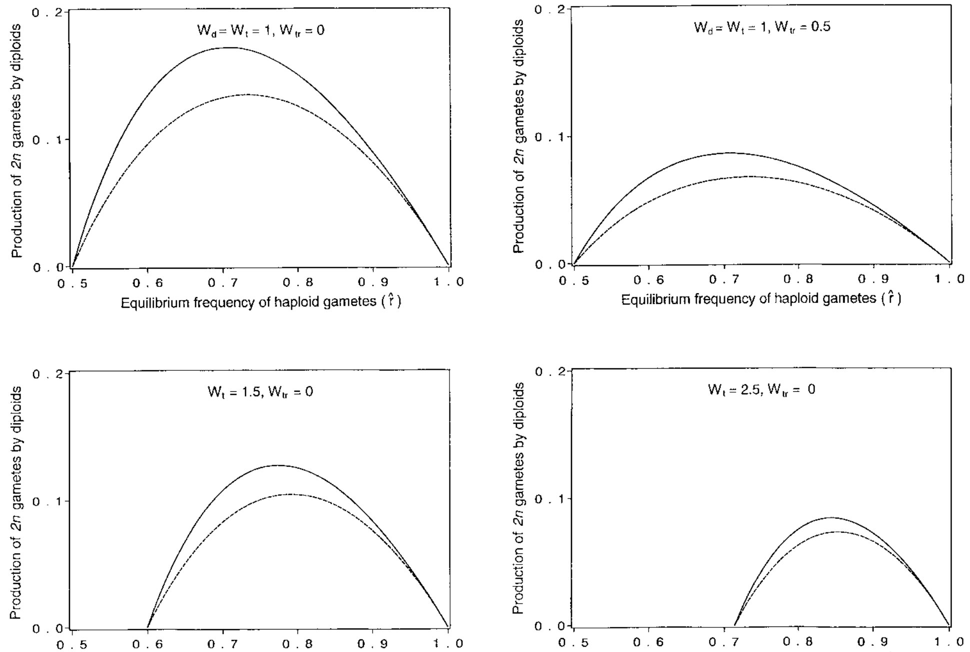

Figure 3. Equilibria frequencies of haploid gametes with and without the assumption of discounting of fitness of diploids in proportion to the rate of 2*n* gamete production. Several values of triploid and tetraploid fitnesses are considered. (——) no discounting, (- - - -) discounting.

DISCUSSION

In the present study, the level of $2n$ gamete production in diploids, the fertility of triploids, and the relative fitness of diploids and tetraploids were found to be major determinants of the dynamics of diploids, triploids and tetraploids. $2n$ gamete production by diploids is an essential factor in the dynamics of cytotype mixtures because they increase the chance of establishment of polyploids and continuously generate polyploids. In fact, when diploids produce $2n$ gametes, a low frequency of tetraploids is maintained in the population even if tetraploids are sterile (Felber, 1991). In this work, we demonstrate that the importance of $2n$ gamete production is not dependent upon the mode of formation of $2n$ gametes. In fact, the effects of $2n$ gamete production are enhanced if their formation results in a proportional reduction in the overall fertility of the diploid. The rate of $2n$ gamete production has been found to increase as a result of environmental conditions. For example, a clone of diploid *Solanum phureja* produced up to 98% of $2n$ gametes under cool uniform conditions and only 57% under warmer and fluctuating temperatures (McHale, 1983). Moreover, dehydration (Giles, 1939), low nutrients (Grant, 1952) and parasites (Sandfaer, 1973), may provoke a dramatic increase in $2n$ gametes production in diploid individuals. This suggests that environmental perturbations may directly influence the probability of establishment of polyploid populations.

The present paper shows that triploids contribute to the establishment of polyploids by decreasing the threshold of $2n$ gametes necessary for the exclusion of the diploids when tetraploids are more fit than diploids. Conversely, if the fitness of diploids is higher than that of tetraploids, then increasing triploid fitness promotes the maintenance of diploids.

In the present model, we assume that triploids produce equal proportions of haploid and diploid gametes. Unfortunately, this assumption cannot be evaluated using available data. While triploids have been used in backcross studies by several scientists (Ledingham, 1940; Jones & Borrill, 1962; Vardi, 1971, 1974; Taylor & Chen, 1988, Pickering *et al.*, 1994), translation of these results into estimates of relative production of haploid and diploid gametes requires knowledge of the relative cytotype fitness and such knowledge is currently unavailable for these systems. Theoretically, the production of a higher proportion of one type of gamete by a triploid would favour it in the population.

Estimates in natural populations of the relative fitness of the cytotypes is sparse. Fitness may be broken up into multiple elements describing vegetative growth or reproductive success. We calculated the relative fitness of cytotypes on data collected in natural mixed populations for *Plantago media* (Van Dijk *et al.*, 1991a) and two grass species, *Dactylis glomerata* (Lumaret *et al.*, 1987) and *Anthoxanthum alpinum* (Felber, in press) (Table 1). Relative fitness of tetraploids based on vegetative growth are lower for tetraploids than for diploids. When reproductive output is considered, fitness estimates are higher for tetraploids than for diploids, with the exception of the shady habitat of *D. glomerata* where the low fitness of tetraploids was explained by unfavourable environmental conditions (Lumaret *et al.*, 1987). Data on *P. media* demonstrate a large interpopulation variation of fitness. Thus, fitness estimates based on reproductive output demonstrate that tetraploids may have either a higher or a lower fitness than the diploids, depending parly on their ecological requirements.

While the viability and partial fertility of triploids has been frequently documented in experimental crosses (Ledingham, 1940; Jones & Borrill, 1962; Taylor & Chen,

TABLE 1. Fitness relative to diploids of triploids (3x) and tetraploids (4x) derived from the data on *Plantago media* (vanDijk *et al.*, 1991a), *Dactylis glomerata* (Lumaret *et al.*, 1987) and *Anthoxanthum alpinum* (Felber, in press)

			Fitness					
			Vegetative growth		Reproductive growth		Reproductive output	
Species	Site	Frequency of triploids (%)	3x	4x	3x	4x	3x	4x
P. media[1]	site 1	2.2	–	0.90	–	0.86	–	1.20
	site 2	0	–	0.95	–	1.03	–	3.30
D. glomerata[2]	site 1	0	–	0.90	–	1.00	–	1.65
	site 2	0	–	–	–	1.40	–	1.85
	site 3	0	–	0.66	–	0.60	–	0.55
A. alpinum[3]	site 1	0.83	0.50	0.85	0.79	1.09	0.77	1.20

[1] vegetative growth (v.g.) = number of leaves; reproductive growth (r.g.) = number of spikes; reproductive output (r.o.) = number of seeds by plant. Fitnesses were calculated between diploids and tetraploids of the same population.

[2] v.g. = number of tillers; r.g = number of panicles; r.o. = number of caryopses; relative fitness is calculated in relation to diploids of site 3, which are the only diploids in the list. The mean was calculated when data was available for two years.

[3] v.g. = id.; r.g. = number of panicles; r.o. = number of caryopses able to germinate by plant.

1988) and nature (Zohary & Nur, 1959), few studies have measured the fitness of triploids relative to that of diploids and triploids. Triploids were present in the well studied population of *P. media* (Van Dijk *et al.*, 1991a), but their fitnesses were not measured. However, at the zone of contact between diploid and tetraploid populations of *A. alpinum* in the Swiss Alps, triploids had a non-negligible fitness relative to diploids of 0.77 (in terms of reproductive output) and occurred at a frequency of 0.83% (Felber, in press). Moreover, tetraploids at this site had a higher fitness than the diploids when considering reproductive growth and output. Consequently, according to our present model, we estimate that the direction of evolution at the hybrid zone is towards an advantage to tetraploids. Thus, the direction of future change in this zone might be towards an increase of tetraploids and a decrease of diploids. However, the cytotypes are known to have a non-random spatial distribution and have differentiated habitats (Felber-Girard *et al.*, 1996). These factors are also likely to be important determinants of the dynamics of the cytotypes. These data emphasize the validity of including triploids in theoretical considerations on the establishment of polyploids and that more fitness estimates on natural populations are needed in order to have a proper evaluation of relative fitness of the cytotypes.

CONCLUSIONS

There is a paradox between the constraints on the establishment of polyploid taxa and the prevalence of polyploidy in flowering plants. The importance of polyploidy is assessed both by its wide occurrence (Stebbins, 1971) and the evidence of recurrent polyploidization (Soltis & Soltis, 1993). While several polyploid taxa (mainly allopolyploids) have originated in historical time as a consequence of human disturbance (Abbott, 1992), many of such taxa are probably of more ancient origins (Favarger, 1984). Therefore, it is likely that a long period has often passed from the origin of given diploid taxa to the present time for differentiating polyploid taxa. This may explain the high frequency of polyploids even with a low probability of success of polyploidization events.

The conditions of establishment of polyploids are manifold and theoretical work has shown that autogamy (Levin, 1975), niche differentiation in a broad sense (Fowler & Levin, 1984), flowering time differentiation (Van Dijk & Bijlsma, 1994), and 2*n* gametes (Felber, 1991) promote the establishment of polyploids. Furthermore, stochastic fluctuations in population size might occasionally allow the tetraploids to spread to fixation (Fowler & Levin, 1984). The present study shows that triploid fitness may play a determinant role in the coexistence of several cytotypes in a single population by modifying their equilibrium values in favour of the diploid or of the tetraploid, depending on their relative fitness.

Theoretical studies on the coexistence of polyploids allow a better interpretation of empirical data. Further studies of each kind are required in the future to obtain a deeper understanding of the predominance of polyploidy among flowering plants.

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