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The Time and Duration of Meiosis [and Discussion]

M. D. Bennett, K. R. Lewis and D. J. Harberd

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The time and duration of meiosis

By M. D. Bennett
Plant Breeding Institute, Maris Lane, Trumpington, Cambridge CB2 2LQ

Ever since meiosis was recognized as a process there has been a continuing interest in its temporal aspects. Two main types of meiotic timing experiments have been conducted: first, experiments to estimate the duration of meiosis (and sometimes its stages); second, experiments to locate the sensitive stage(s) when exposure of meiocytes to various treatments can affect meiotic chromosome behaviour (e.g. pairing or recombination). Such experiments have played an important rôle in increasing our understanding of the meiotic process.

The duration of meiosis has been estimated in about 70 organisms, including two prokaryotes (yeast and *Chlamydomonas*) and the following eukaryotes: 1 Basidiomycete (*Coprinus lagopus*), 2 Gymnosperms (*Larix decidua* and *Thuja plicata gracilis*), at least 39 angiosperms, and at least 26 animal species. The duration of female meiosis has been estimated in far fewer species than male meiosis. However, estimates of the duration of female meiosis are available for 6 angiosperms, *Drosophila melanogaster*, *Xenopus laevis*, and several mammals. Comparison of these data shows that the duration of meiosis is one of the most variable aspects of the meiotic process, ranging from less than 6 h in yeast to more than 40 years in the human female. Developmental holds at different stages of meiosis are common in plants and animals, and inevitably prolong the meiotic division. However, even among species without developmental holds, the duration of meiosis is very variable. For instance, in animals it ranges from about 1–2 days in male *Drosophila melanogaster* to more than 24 days in male *Homo sapiens* and several Orthopterans.

Despite the large variation in the duration of meiosis three generalizations can be made: (i) first prophase is always very long compared with the remaining meiotic stages, (ii) the rate of meiotic development is very slow compared with the rate of development in dividing somatic meristem cells of the same organisms under the same conditions, (iii) the duration of meiosis is characteristic of the genotype and species.

Four main factors have been recognized which effect or determine the duration of meiosis, namely (1) environmental factors (e.g. temperature); (2) nuclear DNA content; (3) ploidy level of the organism; and, (4) the genotype.

Because nuclear DNA content plays a major role in determining the duration of meiosis, it has been suggested that DNA influences the rate of meiotic development in two ways: first through its informational content (the genotype), and second indirectly by the physical and mechanical effects of its mass independently of its informational content (i.e. the nucleotype). Thus, the observed duration of meiosis is the result of a complex genotype–nucleotype–environment interaction.

With the obvious exception of variation caused by developmental holds, changes in the duration of meiosis usually involve proportional changes in the durations of all its stages. This is true irrespective of whether the variation in meiotic time is associated with changes in temperature, nuclear DNA amount, ploidy level, or sex difference. While results for animal species show some evidence of a similar phenomenon, the relative proportions of meiosis taken by individual meiotic stages is clearly much more variable between animal species than between plants.

The duration of meiosis often has much wider implications for the organism than those affecting the meiotic process *per se*. Examples are given from which it is concluded, first, that the duration of meiosis can limit the type of life cycle which a species can display; and second, that in many species the duration of the meiosis is an essential adaptive feature suited to its life cycle type in its normal environment.

1. Introduction

Once meiosis was recognized as a process, cytological studies using many widely unrelated organisms showed that it invariably consisted of the same stages, occurring in the same order. Moreover, that the impressive regularity of the temporal sequence of meiotic events had an important functional significance was soon recognized. Thus, for example, Darlington (1940) wrote that meiosis has 'a uniformity of form and action'.

Apart from concern regarding the number and order of meiotic stages, there has been a considerable and continuing interest in temporal aspects of the meiotic process. As a result, two main types of meiotic timing experiments have been conducted. First, there have been many experiments to estimate the duration of meiosis (and sometimes its stages). Second, there have been many experiments to locate the position of the sensitive stage(s) when exposure of meiocytes to various treatments can affect meiotic chromosome behaviour (for example, chromosome pairing or recombination). A third class of meiotic timing experiments has combined both of the above types of experiments so that the sensitive stage(s) has been identified with a particular part of meiocyte development.

(*a*) *Experiments to time the duration of meiosis and its stages*

A review of some of the methods and techniques used to estimate the duration of meiosis has already been made (Bennett 1971). The methods used to estimate the duration of meiosis are of two main types, namely non-autoradiographic methods and autoradiographic methods.

(i) *Non-autoradiographic methods*

These depend upon the existence of either a precise relation between the stage of meiotic development and the size of a reproductive organ, or, a high degree of synchrony during meiotic development in a population of meiocytes which can be sampled at intervals without affecting the rate of development in the remaining meiocytes. Thus, in an early experiment utilizing the relation between bud length and meiotic development Sax & Edmunds (1933) showed that male meiosis lasted 5 or 6 days in *Tradescantia reflexa* by marking the buds with Indian ink and making smears each day from buds of the same size from the same plant. Later Erickson (1948) used the relation between bud length and stage of pollen mother cell (p.m.c.) development, and knowledge of the rate of increase in bud length, to estimate the duration of male meiosis in *Lilium longiflorum* cv. Floridi. Recently, a similar method was used by Bennett & Stern (1975*a*, *b*) to estimate the duration of male and female meiosis and of the preleptotene chromosome condensation stage in *Lilium* cultivars.

Alternatively, meiosis has been timed in many higher plant species by sampling p.m.cs from a synchronous population at differing known intervals. This method is especially suited to species with two or more synchronously developing anthers per floret. An early meiotic timing experiment using this method was carried out by Ernst (1938) to show that meiosis in *Antirrhinum majus* lasted about 24 h. This method has continued to be used for suitable plant species until the present day having been applied to *Endymion nonscriptus* (Wilson 1959), and numerous cereal species including, wheat, rye, barley and *Triticale* (Bennett, Chapman & Riley 1971; Bennett & Smith 1972; Finch & Bennett 1972; Bennett & Kaltsikes 1973). The method has been subject to many modifications involving sampling of whole or parts of anthers (either attached to the plant or in culture) and even cultured columns of p.m.cs of *Lilium* and *Trillium*

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extruded from anthers into White's medium (Ito & Stern 1967). Timing meiosis by sampling at intervals from a large synchronous population of meiocytes has also been possible in the Basidiomycete, *Coprinus lagopus*. This fungus has a fruiting body with about 100 gills, each of which is at an identical stage of development, and each of which possesses hundreds of thousands of basidia in very close synchrony for meiotic stage (Lu 1967). Each gill can be removed at any time during meiotic development without interfering with normal morphogenesis of the fruiting body; thus samples can be taken at many different times giving 'a live coverage of meiotic events' (Lu 1969). Development from karyogamy to tetrad stage in *Coprinus lagopus* took about 16 h (Raju & Lu 1970). Experiments which use non-autoradiographic methods have been almost entirely limited to a few suitable plant species whose morphology and development, unlike those of nearly all animal species, was amenable to this type of experimental approach.

(ii) *Autoradiographic methods*

The development of autoradiography made it possible to time meiosis in animal species and in those plant species whose morphology and development were not suited to the methods outlined above. Timing meiosis using autoradiography involves pulse labelling nuclei with precursors at premeiotic DNA synthesis and then following the progress of a wave of cells with labelled meiotic chromosomes into successively later stages of meiosis in tissue fixed at known intervals after labelling. This method has been successfully applied to prokaryotes, for example, *Saccharomyces cerevisiae* (Piñon *et al.* 1973) and *Chlamydomonas reinhardi* (Lawrence 1965) as well as to many eukaryotes. Moreover, the method has made it possible to time female meiosis as well as male meiosis in several animal species. Use of autoradiographic methods for timing meiosis had important advantages besides those mentioned above. First, it showed that chromosome replication occurred before the start of meiosis. Second, it provided a new stage (premeiotic DNA synthesis stage) which could be precisely identified at a period of meiocyte development when stage identification based on the features visible in the light microscope is very difficult. Thus, in many species it allowed the start of meiosis to be more accurately determined.

(*b*) *Experiments to locate treatment sensitive stages*

Many treatments (including notably temperature, radiation and colchicine) are known which can affect meiotic chromosome pairing and recombination, as judged by a difference in chiasma frequency or rate of recombination between treated and untreated meiocytes. One of the earliest papers noting such an effect of temperature in *Drosophila* was published by Plough (1917). Experiments to locate the position of a sensitive stage relative to first metaphase usually involve either a short 'shock' exposure to a treatment known to affect pairing; or, switching meiocytes from continuous exposure to a treatment at which chromosome pairing is normal to continuous exposure to another treatment known to reduce or enhance pairing (for examples see Barber 1942; Lamb 1969; Bayliss & Riley 1972*a*, *b*). Results of early experiments to determine the location of the sensitive stage were of limited value. Even though they showed that the sensitive stage was so many hours prior to first metaphase, it was often still unclear whether the sensitive stage was premeiotic or meiotic because no precise data concerning the duration of meiosis and its stages were available. For example, Barber (1942) located both a temperature and a colchicine sensitive stage in *Fritillaria meleagris*, the former of short duration about 1–2 days prior to first metaphase, and the latter more than 3 weeks prior to first metaphase. While Barber could be reasonably sure that the temperature sensitive stage occurred at pachytene

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he could not be sure whether the colchicine sensitivity coincided with a particular stage of first meiotic prophase nor even whether it occurred at premeiotic interphase or during meiosis.

(*c*) *Experiments combining timing meiosis with locating sensitive stages*

In recent years many meiotic timing experiments have attempted both to estimate the duration of meiosis, and to locate sensitive stages at which meiotic chromosome behaviour can be affected by various treatments. For instance, Henderson (1966) carried out two experiments involving the heat-treatment of *Schistocerca gregaria* males immediately after injecting them with [^{3}H]thymidine. Autoradiographs and chiasma frequency scores enabled him to compare the time taken by labelled cells to move through meiosis, with the periods during which chiasma frequencies were modified by heat-treatment. As the result of such experiments premeiotic and meiotic stages at which chromosome pairing and recombination can be affected by various treatments have been carefully identified with several individual stages of development including premeiotic G1 (Bayliss & Riley 1972*a*; Dover & Riley 1973), premeiotic DNA synthesis (Grell & Chandley 1965; Lu 1974), leptotene-zygotene (Church & Wimber 1969*b*; Raju & Lu 1973), and zygotene-pachytene (Peacock 1968; Parchman & Stern 1969). Detailed studies of this type have been made using several plant and animal species including, yeast, *Chlamydomonas*, *Coprinus*, *Neurospora*, bread-wheat, *Lilium* ssp., *Drosophila*, and several grasshopper species. Such experiments have played an important role in increasing our understanding of the meiotic process. As this work will not be discussed further in this review the reader is referred to the following papers: Lawrence (1961*a*, *b*), Grell (1966), McNelly-Ingle, Lamb & Frost (1966), Westerman (1967), Henderson (1966, 1970), Chandley (1968), Maguire (1968), Lamb (1969), Lu (1969), Peacock (1970), and Buss & Henderson (1971).

2. The duration of meiosis

(*a*) *The available data*

Many of the early meiotic timing experiments were understandably imprecise using, for instance, plants growing in uncontrolled and undefined environmental conditions in the field or greenhouse. Consequently, the results obtained are of limited use. However, recent experiments have usually been conducted under closely defined and controlled conditions, and have provided considerable data on the duration of meiosis from which useful conclusions may be drawn.

To date, the duration of meiosis (and sometimes its stages) has been estimated in at least 70 different species including two prokaryotes, *Saccharomyces cerevisiae* (Piñon *et al.* 1973) and *Chlamydomonas reinhardi* (Lawrence 1965); a Basidiomycete, *Coprinus lagopus* (Raju & Lu 1970); two gymnosperms, *Larix decidua* (Ekberg & Eriksson 1967) and *Thuja plicata gracilis* (Simak, Gustafsson & Rantenberg 1974); at least 39 angiosperms (table 1) and at least 26 animal species (table 2).

In both plant and animal species with two track heredity there are many more published data on the duration of male meiosis than for female meiosis. This undoubtedly reflects the greater ease with which male meiocytes can be located and handled in meiotic timing experiments in most species. Nevertheless, the duration of meiosis has been estimated in at least six species of higher plants (table 7), and several animal species (see §5*b*). Throughout this review, unless otherwise stated, results and conclusions will refer to male meiosis.

TABLE 1. THE DURATION OF MALE MEIOSIS, NUCLEAR DNA CONTENT, PLOIDY LEVEL AND CHROMOSOME NUMBER IN 39 ANGIOSPERM TAXA (MODIFIED FROM BENNETT 1976)

species		reference to meiotic timing	duration of meiosis / h	3*C* nuclear DNA content / pg	chromosome number
Diploids					
1. *Petunia hybrida*		Izhar & Frankel 1973	18	5.7	14
2. *Beta vulgaris*		Bennett 1973	24	4.1	18
3. *Antirrhinum majus*		Ernst 1938	24	5.5	16
4. *Haplopappus gracilis*		Marithamu & Threlkeld 1966	24–36	5.5	4
5. *Vicia sativa*		Bennett 1976	24	8.2	12
6. *Lycopersicum esculentum*		Bennett 1973	24–30	8.5	24
7. *Pisum sativum*		Bennett 1976	30	14.8	14
8. *Ornithogalum virens*		Church & Wimber 1969	72	19.3	6
9. *Hordeum vulgare* cv. 'Sultan'		Bennett & Finch 1971	39	20.3	14
H. vulgare cv. 'Ymer'		Finch & Bennett 1972	39	20.3	14
10. *Triticum monococcum*		Bennett & Smith 1972	42	21.0	14
11. *Rhoeo discolor*		Vasil 1959	48	23.8	12
12. *Secale cereale*		Bennett *et al.* 1971	51	28.4	14
13. *Vicia faba*		Maquardt 1951	72	44.0	12
14. *Allium cepa*		Vasil 1959	96	50.3	16
15. *Tradescantia paludosa*		Stenitz 1944; Taylor 1949, 1950; Beatty & Beatty 1953	126	54.0	12
16. *Tulbaghia violacea*		Taylor 1953	130	58.5	12
17. *Endymion nonscriptus*†		Wilson 1959	48	69.9	16
18. *Convallaria majalis*†		Bennett 1973	72	81.3	38
19. *Lilium henryi*		Pereira & Linskins 1963	170	100.0	24
20. *L. longiflorum*		Taylor & McMaster 1954; Ito & Stern 1967	192	106.0	24
21. *L. candidum*		Sauerland 1956	168	—	24
22. *L. hybrid* cv. 'Black Beauty'		Bennett & Stern 1975	264	—	24
23. *Trillium erectum*		Ito & Stern 1967	274	120.0	10
24. *Fritillaria meleagris*		Barber 1942	400	233.0	24
Polyploids					
25. *Lilium hybrid* cv. 'Sonata'	(3×)	Bennett & Stern 1975	180	—	36
26. *Capsella bursa-pastoris*	(4×)	Bennett 1973	18	2.6	32
27. *Veronica chamaedrys*	(4×)	Bennett 1973	20	2.8	28
28. *Alliaria petiolata*	(4×)	Bennett 1973	24	7.1	36
29. *Triticum dicoccum*	(4×)	Bennett & Smith 1972	30	38.5	28
30. *Hordeum vulgare* cv. 'Ymer'	(4×)	Finch & Bennett 1972	31	40.6	28
31. *Triticale turgidum* var. *durum*	(4×)	Bennett & Kaltsikes 1974	31	37.9	28
32. *T. aestivum* × *S. cereale* (polyhaploid)	(4×)	Bennett 1973	35	41.8	28
33. *T. aestivum* × *Ae. mutica*	(4×)	Bennett, Dover & Riley 1974	31	42	28
34. *Secale cereale*	(4×)	Bennett *et al.* 1971	38	56.8	28
35. *Tradescantia reflexa*	(4×)	Sax & Edmonds 1933	144	144.9	24
36. *Triticum aestivum* cv. 'Chinese Spring'	(6×)	Bennett *et al.* 1971	24	54.3	42
37. *T. aestivum* cv. 'Holdfast'	(6×)	Bennett *et al.* 1972	24	54.3	42
38. *Triticale* cv. 'Rosner'	(6×)	Bennett & Smith 1972	35	66.3	42
39. *Triticale* genotype A	(8×)	Bennett & Smith 1972	21	82.7	56
genotype B	(8×)	Bennett & Smith 1972	22	82.7	56

The duration of meiosis was measured at 18 °C in species 8, and at 20 °C in species 2, 5, 6, 7, 9, 10, 12, 16, 17, 18, 20, 22, 25, 33, 34, and 36–38. No temperature was given for species 3, 4, 11, 13, 14, 15, 19, 21 and 35. Species 23 was measured at 15 °C; species 24 at 12–15 °C; and species 1 at 15–17 °C at night and 25–30 °C during the day. The expected meiotic time at 20 °C is given assuming a meiotic Q_{10} of 2.3. The values for species 8, 13 and 24 are only approximate although of the right order.

† Species marked behave as tetraploids with respect to meiotic time (Bennett 1973) and consequently they are not plotted as diploids in figure 2.

DNA amounts are taken from Bennett (1972).

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TABLE 2. THE DURATION OF MALE MEIOSIS AND 2*C* NUCLEAR DNA CONTENT IN 26 ANIMAL SPECIES

species	reference to timing	temperature/°C	2*C* DNA amount	duration of meiosis/ days	duration of first prophase of meiosis/ days
Turbellaria					
1. *Urecho caupo*	Nelson 1971	—	—	3–4	—
Gastropoda					
2. *Helix aspersa*	Block & Hew 1960	not given	—	12.3	—
Insecta					
3. *Acheta domesticus*	Lyapunova & Zosimovskaya 1973	—	—	10–14	9–11
4. *Chorthippus brunneus*	Craig-Cameron & Jones 1970	30	20.0	8.5	—
5. *C. parallelus*	Fox, Hewitt & Hall 1974	mean 26 (23/29)	28.8	20.0	19
6. *C. vagans*	Craig-Cameron & Jones 1970	30	—	9.5	—
7. *Drosophila melanogaster*	Chandley & Bateman 1962	not given	0.085	1–2	—
8. *Euthystira brachyptera*	Craig-Cameron & Jones 1970	30	—	15–17	14–16
9. *Goniaea australiasiae*	Peacock 1968, 1970	37	—	14	13
	Peacock 1968, 1970	26	—	*ca.* 30	
10. *Locusta migratoria*	Buss & Henderson 1971	30	12.8	7–8	7
	Buss & Henderson 1971	40	—	3.5–4	> 3
11. *Melanoplus differentialis*	Muckenthaler 1964	35	—	9.0	—
	Henderson 1970	39	—	*ca.*8.0	—
12. *M. femur-rubrum*	Church & Wimber 1969*b*	42	—	9.0	8
13. *Myrmeleotettix maculatus*	Fox, Hewitt & Hall 1974	mean 26 (23/29)	28.4	19–22.5	18
14. *Romalea microptera*	Taylor 1965	20–25	—	24–26	24
15. *Schistocerca gregaria*	Henderson 1966	30	20.0	14	12–13
	Henderson 1966	40	20.0	6	5
	Westerman 1967	not given	20.0	7.5	6.5
	Craig-Cameron 1970	—	20.0	—	—
16. *Sciara coprophila*	Rieffel & Crouse 1966	20	—	1–2	—
17. *Stenophyma grossum*	Jones 1971	30	—	11.5–12.5	11.5
Amphibia					
18. *Triturus viridescens*	Wimber & Prensky 1963	20–22	72.0	12–13	12
19. *T. vulgaris*	Callan & Taylor 1968	16	67.9	21	20
Mammalia					
20. *Cricetulus griseus*	Utakoji 1966	near body heat	—	20–24	20
21. *Homo sapiens*	Heller & Clermont 1963		6.0	24	—
22. *Mesocricetus auratus*	Ghosal & Mukherjee 1971		—	11.5–12.5	11
23. *Mus musculus*	Kofman-Alfaro & Chandley 1970		5.0	12	> 10.5
	Ghosal & Mukherjee 1971		5.0	11–12	11
24. *Oryctolagus*	Swierstra & Foote 1965		5.3	17	—
25. *Ovis*	Ortavant 1956		5.7	17	> 15
26. *Rattus*	Clermont, LeBlond & Messier 1959		5.7	18	—

DNA amounts for species 4, 5, 10, 13 and 15 are from John & Hewitt (1966); for species 7 from Sager & Ryan (1961); for species 18 and 19 from Swift (1958) and Ullerich (1970); and for species 21, 23, 24, 25 and 26 from Vendrely (1955) and Wiley & Yunis (1975).

(*b*) *Variation in the duration of meiosis*

The duration of meiosis is one of the most variable aspects of the meiotic process, ranging from an observed minimum of less than 6 h in *Saccharomyces cerevisiae* (Piñon *et al.* 1973) to a maximum of more than 40 years in the human female. This comparison is somewhat unfair, since it contrasts times for an organism completing meiosis without a developmental hold

(yeast) with an organism which has a prolonged developmental hold during meiosis (the human female). Nevertheless, the duration of meiosis is very variable even between species lacking any obvious developmental hold during meiosis. For instance, it ranges from 1–2 days in *Drosophila melanogaster* to more than 20 days in several Orthopterans and man (see table 2). Similarly, in angiosperms it ranges from less than 24 h in *Petunia* hybrids (Izhar & Frankel 1973) to about 3 months in *Trillium* (Hotta & Stern 1963*a*), while, even in plants all grown at a constant 20 °C, it varies from about 18 h in *Capsella bursa-pastoris* (Bennett 1973*a*) to about 10.5 days in *Lilium* hybrid cv. Black Beauty (Bennett & Stern 1975*a*).

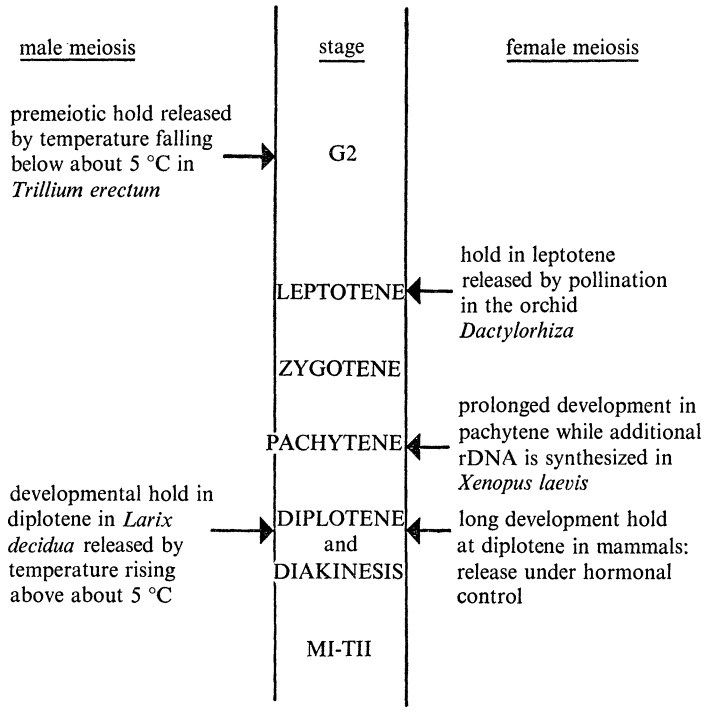

FIGURE 1. Developmental holds occurring at different stages of the meiotic cycle in male or female meiocytes of several plant and animal examples.

Developmental holds during the meiotic cell cycle are common in plant and animal species, and their action inevitably increases the time spent in meiosis. Developmental holds are known which occur at many different stages of the meiotic cell cycle (some examples are given in figure 1). Thus, developmental holds have been recognized at premeiotic interphase in *Trillium erectum* (Hotta & Stern 1963), at leptotene in embryo sac mother cells (e.m.c.) of the orchid *Dactylorhiza* (Heslop-Harrison 1957), at pachytene in female *Xenopus laevis* (Bird & Birnstiel 1971; Coggins & Gall 1972), and at diplotene in *Larix decidua* (Ekberg & Erickson 1967) and many female mammals (Edwards 1965). Identical developmental holds may occur in male and female meiocytes of the same species, or they may occur in only one track of heredity. An example of the latter is seen in the orchid *Dactylorhiza* where it is the e.m.cs which are held at leptotene until pollination occurs (Heslop-Harrison 1957). Similarly, in human males meiosis occurs continuously during many years of sexual maturity, taking about 24 days in each individual spermatocyte (Heller & Clermont 1963), while in females the stages of meiosis up until diplotene are completed before birth. Thereafter, oocytes are held in the dictyate condition

at late first meiotic prophase for many years before being released sequentially by the action of luteinizing hormone. Once released oocytes develop quickly to second metaphase (in about 40 h) when there is a second delay until ovulation occurs and the egg enters the fallopian tube. Fertilization then provides the stimulus for the completion of the second meiotic division (Edwards 1965).

While meiotic divisions may be subdivided usefully into those with and those without developmental holds, clearly there is no fundamental difference between the meiotic process in meiocytes with the two types of development. The occurrence of a developmental hold reflects the action of an optional control of meiocyte behaviour superimposed upon the mandatory sequence of events which are essential for completion of the meiotic process. Thus, developmental holds occurring during meiosis have no significance for the meiotic process, instead they indicate adaptation related to the peculiar needs of reproductive development or of the life cycle (see also §7). Developmental holds are released in various organisms in response to light (Ninnemann & Epel 1973; Lu 1974), temperature and hormonal stimulation. Moreover, the same temperature treatment (exposure to temperatures below about 5 °C) induces meiotic dormancy in one species, *Larix decidua*, but breaks dormancy in another, *Trillium erectum*. Clearly, therefore, no great significance should be attached to the nature of the condition required to release a developmental hold other than to recognize that each species is adapted so that meiosis occurs at the optimum time in the life cycle for individuals living in their normal environment.

Despite the large variation in the duration of meiosis both within and between species, nevertheless, three generalizations can be made:

(1) First meiotic prophase is usually very long compared with the remaining stages of meiosis. For instance, in *Secale cereale* first prophase lasted about 41 h out of a total meiotic time of about 51 h (Bennett *et al.* 1971), while in *Romalea microptera* it lasted about 23 days out of a total meiotic duration of about 24 days (Taylor 1965).

(2) The rate of cell development in meiocytes is much slower than in dividing non-meiotic cells of the same organism in the same environmental conditions (Bennett 1971). Thus, the vegetative cell doubling time in *Saccharomyces cerevisiae* at 25 °C is about 2.5 h (Williamson & Scopes 1961) while the meiotic cycle lasts about 10 h (Piñon *et al.* 1973). Similarly, the maximum rates of somatic cell division in mouse and man are about 9.5 and 19 h respectively (Moore 1971), while the duration of the meiotic cycle is greater than about 12 and 24 days, respectively. The duration of the meiotic cycle from premeiotic mitosis to first telophase of meiosis in *Triticum aestivum* and *Lilium longiflorum* is about 3 and 9 days, respectively, at 20 °C, while the durations of root-tip meristem cell cycles in these two species are about 12 and 24 h, respectively (Bennett 1976). The meiotic cycle is known to contain a prolonged DNA synthesis phase (S) compared with non-meiotic cell cycles in several widely unrelated species including, yeast (compare Williamson & Scopes 1961 and Simchen, Salts & Piñon 1973), wheat (Bennett *et al.* 1971), mouse (Monesi 1962; Lima-de-Faria & Borum 1962) and newt (Callan 1972). However, the increased duration of the meiotic cycle compared with non-meiotic cycles is not the result of increased S-phase alone (Bennett 1971; Bennett & Smith 1972). Thus, the duration of the first meiotic division (leptotene to first telophase inclusive) is greatly prolonged compared with the duration of mitosis. For instance, in *Triticum aestivum* at 20 °C, the first meiotic division lasts about 19.5 h while mitosis in root-tip meristem cells takes about 1.2 h. Moreover, although the duration of first prophase (17 h) is long compared with prophase in root-tip cells (about

0.5 h), the extended duration of the meiotic cycle cannot be explained just in terms of the additional chromosome activities (pairing and recombination) occurring during the former but not the latter. Thus, even for strictly corresponding stages, the duration is greatly prolonged during meiotic compared with mitotic cycles. For instance, in root-tip cells of *Triticum aestivum* cv. Chinese Spring, metaphase to telophase inclusive takes about 0.6 h (M. W. Bayliss, unpublished) while in p.m.cs, first metaphase to first telophase takes about 2.6 h and second metaphase to second telophase about 2.4 h (Bennett *et al.* 1971) at 20 °C.

Data for several species show that the slow rate of meiotic cell development is not the result of a sudden change in rate of development but is preceded by a gradual change in the rate of development spread over several cell cycles preceding meiosis (Monesi 1962; Bennett, Finch, Smith & Rao 1973).

TABLE 3. THE DURATION OF MEIOSIS AND POLLEN MATURATION IN DIFFERENT GENOTYPES OF SEVERAL HIGHER PLANT SPECIES

species	duration of meiosis / h	temperature / °C	pollen maturation time / days
1. *Hordeum vulgare* cv. Sultan	39	20	—
2. *H. vulgare* cv. Ymer	39	20	—
3. *Lilium longiflorum* cv. Croft	*c.* 192	23	—
4. *L. longiflorum* cv. Floridii	*c.* 240	not given	—
5. *L. longiflorum* cv. Nellie White	*c.* 192	22	—
6. *Secale cereale* cv. Petkus Spring	51	20	16.0
7. *S. cereale* cv. Prolific	51	20	16.0
8. 6× *Triticale* cv. Rosner	34	20	10.0
9. 6× *Triticale* cv. 6A 190	37	20	10.0
10. 8× *Triticale* cv. CS/K-TA	21	20	—
11. 8× *Triticale* cv. CS/Pet-TA	22	20	—
12. *Triticum aestivum* cv. Chinese Spring	43	15	13.5
13. *T. aestivum* cv. Chinese Spring	24	20	—
14. *T. aestivum* cv. Holdfast	45	15	13.0
15. *T. aestivum* cv. Holdfast	25	20	—

References from which data are collated: 1, Bennett & Finch (1971); 2, Finch & Bennett (1972); 3, Taylor & McMaster (1954); 4, Erickson (1948); 5, Ito & Stern (1967); 6–9, Bennett & Kaltsikes (1973); 10 and 11, Bennett & Smith (1972); 12–15, Bennett, Smith & Kemble (1972).

TABLE 4. THE DURATION OF THE SEMINIFEROUS EPITHELIAL CELL CYCLE, OF MEIOSIS, AND OF SPERMATOGENESIS IN DIFFERENT GENOTYPES OF THE SAME ANIMAL SPECIES

species	temperature / °C	seminiferous epithelial cell cycle / h	meiosis / days	spermatogenesis / days
1. *Mus musculus* (a random bred Q strain from Dr A. McLaren)	near body heat	—	*ca.* 13	—
2. *M. musculus* line C57 BL/6J	near body heat	—	*ca.* 12	—
3. *Rattus* Sprague Dawley	near body heat	12.9	—	49
4. *Rattus* Wistar	near body heat	13.3	—	49
5. *Schistocerca gregaria*	40	—	*ca.* 6	—
6. *S. gregaria*	38	—	*ca.* 7.5	—
7. *S. gregaria*	not given	—	*ca.* 7.0	—

References from which data are collated: 1, Kofman-Alfaro & Chandley (1970); 2, Ghosal & Mukherjee (1971); 3, 4, Nelson (1971); 5, Henderson (1966); 6, Craig-Cameron (1970); 7, Westerman (1967).

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(3) The duration of meiosis is characteristic of the genotype and species cultured under constant environmental conditions. This fact is implicit in the methodology of many meiotic timing experiments, for instance, those where individuals are sampled at intervals from a population all labelled with [^{3}H]thymidine at the same time. I have estimated the duration of meiosis in at least four experiments in *Triticum aestivum* cv. Chinese Spring grown at 20 °C, and each time the result obtained was 24 ± 1 h. The duration of meiosis has been estimated in more than one genotype of only a few plant and animal species. Nevertheless, the results for plants (table 3) and animals (table 4) strongly support the conclusion that the duration of meiosis is usually quite constant in different genotypes of the same species. It should be noted that intraspecific constancy of duration applies not only to meiosis but to premeiotic and post-meiotic stages also (table 4). Thus, speaking of the duration of the seminiferous epithelial cycle in mammals Nelson (1971) wrote, 'the duration of the cycle is quite constant for any given species, and does not appear to deviate even in animals subjected to abnormal physiological conditions'.

While constancy is the rule, several exceptions are known, or suspected (Henderson 1970). While there was general agreement between the rates of meiotic development estimated for human spermatocytes *in vivo* (Heller & Clermont 1963) and *in vitro* (Lima-de-Faria *et al.* 1968), there is a suggestion that male meiosis may have a slightly increased duration in older individuals (Lima-de-Faria *et al.* 1968). Also, it has been shown that the rate of meiotic development is much slower in hibernating than in non-hibernating golden hamsters (Smit-Vis & Akkerman-Bellaart 1966). However, these results may only reflect slight changes in environmental conditions (either in culture solution or temperature) known to affect the rate of meiotic development.

3. Factors which affect or determine the duration of meiosis

Four main factors have been recognized which affect or determine the duration of meiosis, namely (1) environmental affects, (2) nuclear DNA amount, (3) ploidy level, and (4) the genotype. This paper will only mention some of the main conclusions regarding these factors but further details are given in other reviews (Bennett 1971, 1973*a*, 1976).

(*a*) *Environmental factors*

As might be expected from similar studies on somatic cells (see table 6, and Sisken, Morasca & Kibby 1965) meiosis is very sensitive to temperature in both plant and animal species (table 5). The duration of meiosis decreases with increasing temperature over the range of temperatures in which each organism can survive. In plants the most complete study was made by Wilson (1959) using *Endymion nonscriptus* in which the duration of meiosis was estimated in plants grown at each 5 °C interval over the range 0–30 °C. In animals the most complete data are for the locust *Schistocerca gregaria* at four temperatures in the range 30–40 °C (table 5). The results show that the Q_{10} for meiosis decreases as temperature is increased. For instance, in *Endymion nonscriptus* the Q_{10} for the intervals 0–10, 10–20, and 20–30 °C were 5.1, 3.5 and 2.2, respectively. Comparison of data for different species suggests that the Q_{10} for a constant 10 °C interval is very similar for both plants and animals. Thus, for the interval 15–25 °C the Q_{10} for meiosis in *Secale cereale*, *Triticum aestivum* and *Endymion nonscriptus* all fall in the range 2.3–2.8. The Q_{10} for meiosis in grasshoppers for 10 °C intervals in the range 26–40 °C are about 2.0–2.3 in *Schistocerca gregaria*, *Locusta migratoria* and *Goniaea australasiae* (Henderson 1966; Buss & Henderson 1971; Peacock

1968, 1970), while in *Endymion nonscriptus* the Q_{10} for the highest 10° interval measured (20–30 °C) was about 2.2. Comparison of the data for meiosis with those for mitotic cycles in somatic tissues shows that for a constant 10 °C interval (15–25 °C) the Q_{10} values obtained for meiosis fall within the range of values obtained for mitotic cycles for the same 10 °C interval (table 6).

TABLE 5. THE DURATION OF MEIOSIS (IN DAYS) AT DIFFERENT TEMPERATURES IN FOUR HIGHER PLANT AND THREE ANIMAL SPECIES

	temperature/°C								
plant species	0	1	2	5	10	15	20	25	30
1. *Triticum aestivum*	—	—	—	—	—	1.79	1.00	0.75	—
2. *Secale cereale*	—	—	—	—	—	3.65	2.12	1.63	—
3. *Endymion nonscriptus*	36	—	—	15	7	3.50	2.00	1.25	0.83
4. *Trillium erectum*	—	90	70	40	—	16	—	—	—

	temperature/°C					
animal species	26	30	32	37	38	40
5. *Goniaea australasiae*	30	—	—	14	—	—
6. *Locusta migratoria*	—	7–8	—	—	—	3.5–4.0
7. *Schistocerca gregaria*	—	14	11	—	7.5	6

Data from the following references: species 1, 2, Bennett, Smith & Kemble (1972); species 3, Wilson (1959); species 4, Hotta & Stern (1963*a*, *b*); Kemp (1964); Ito & Stern (1967); species 5, Peacock (1968, 1970); species 6, Buss & Henderson (1971); species 7, Henderson (1966); Craig-Cameron & Jones (1970).

TABLE 6. THE Q_{10} FOR ROOT-TIP CELL CYCLE TIMES AND MEIOSIS IN SEVERAL ANGIOSPERM SPECIES (FOR THE INTERVAL 15–25 °C)

stage of development	species	reference	Q_{10}
root-tip cell cycle	*Pisum sativum*	Brown 1951	*ca.* 1.6
	Triticum aestivum	Bayliss, unpublished	*ca.* 1.7
	Helianthus annuus	Burholt & Van't Hof 1971	3.0
meiosis	*Endymion nonscriptus*	Wilson 1959	2.8
	Secale cereale	Bennett, Smith & Kemble 1972	2.2
	Triticum aestivum	Bennett *et al.* 1972	2.4

Our knowledge of the effects of environmental factors other than temperature on the duration of meiosis is very scanty. Dehydration and physical damage of anthers appear either to have no effect or to result in the complete cessation of meiotic development (Bennett *et al.* 1971). Walker & Dietrich (1961) suggested that kinetin can speed up late meiotic prophase development in *Tradescantia*.

Studies of the effects of various factors (day-length, light intensity, humidity, CO_2 and oxygen concentration) and chemical treatments on the rate of meiocyte development both *in vivo* and *in vitro* might usefully be made in view of the very limited data available on this subject.

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(*b*) *Nuclear DNA content*

Van't Hof & Sparrow (1963) demonstrated a highly significant positive relation between nuclear DNA content and the minimum cell cycle time in root-tip meristem cells for several diploid angiosperm species grown under constant environmental conditions. Comparisons of widely unrelated diploid angiosperm species have revealed a similar precise relation (figure 2) between nuclear DNA content and the duration of meiosis (Bennett 1971, 1973*a*, 1976). Analysis has shown that there is no effect of the diploid chromosome number on the duration of meiosis. Thus, the major effect of DNA amount on rate of meiotic development is associated with the total mass of DNA per nucleus and not with the mean DNA content per chromosome (Bennett 1971).

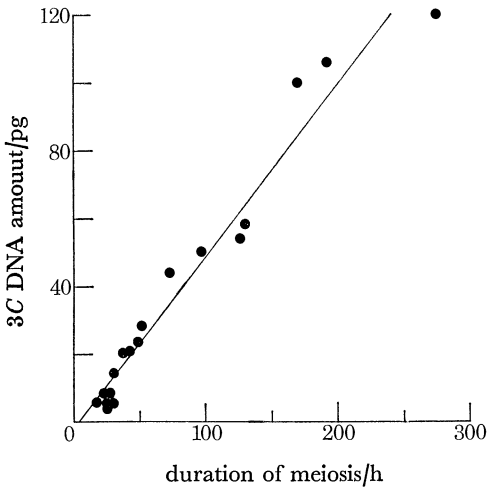

FIGURE 2. The relationship between nuclear DNA content and the duration of meiosis in diploid angiosperms ($P < 0.001$). (N.B. The data plotted are for diploids listed in table 1, nos. 1–24. Species 8 and 24 are omitted because they are only approximate, and species 17 and 18 are omitted because they behave as tetraploids (Bennett 1973).)

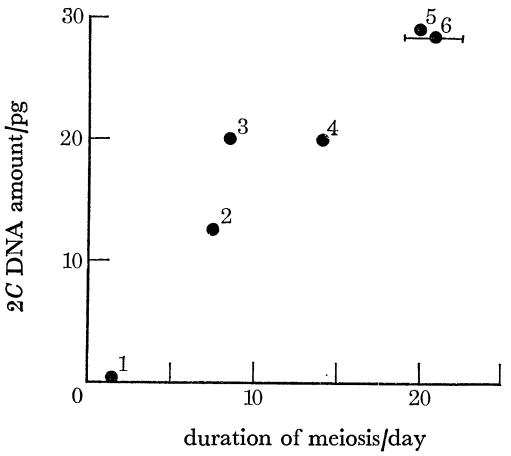

FIGURE 3. The relation between nuclear DNA content and the duration of meiosis for seven insect species ($P < 0.001$; $r = 0.94$). The data plotted are taken from table 2. Key to points: 1, *Drosophila melanogaster*; 2, *Locusta migratoria*; 3, *Chorthippus brunneus*; 4, *Schistocerca gregaria*; 5, *Chorthippus parallelus*; 6, *Myrmeleotettix maculatus*.

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As the result of comparisons of the data for mammals (Bennett 1971) and for insects (figure 3) I suggest that there may be relationships between nuclear DNA content and the duration of meiosis for both these groups similar to that already noted for diploid angiosperms.

Comparing results for plant and animal species show that all the animal species investigated have much longer meiotic divisions than do plant species with corresponding DNA amounts. However, the results for different groups of animals appear to depart from the regression for DNA amount on meiotic duration for diploid plants by different amounts; amphibians showing the least, insects an intermediate, and mammals the greatest departure. Assuming the limited data so far available are typical for the groups of animals which they represent, then it seems reasonable to suggest, first, that the slopes of the regression lines for DNA amount on meiotic time for amphibians, insects and mammals all differ significantly from the slope for angiosperms,

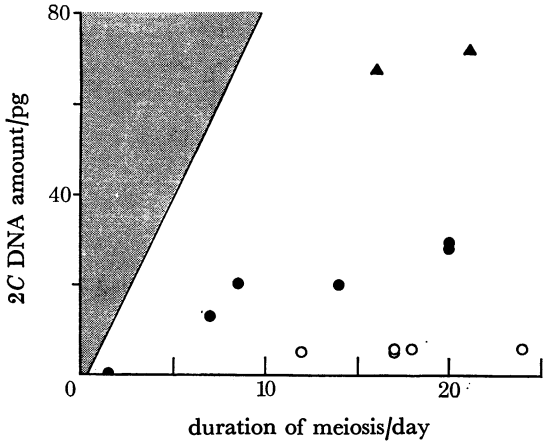

FIGURE 4. The relation between the duration of meiosis in 14 animal species compared with the regression line for diploid angiosperms taken from figure 2. The data for amphibia (▲), insects (●) and mammals (○) are plotted from table 2. (N.B. Points for polyploid plants fall within the shaded triangle between the ordinate and the regression line for diploid angiosperms.)

and second, that after angiosperms, the slopes of the regressions are steepest for the amphibians, less steep for the insects, and least steep for the mammals. If so, then the different slopes would be related to the maximum DNA amount per nucleus for species occurring in each group. Thus, the slope then would be steepest for higher plants which have a maximum *C* value of about 140 picograms (pg) (Bennett 1972), followed by amphibians, insects and mammals with maximum DNA amounts of about 100, 15 and 5 pg, respectively (John & Hewitt 1966; Callan 1972). Further studies should be undertaken for animals to see whether this interesting idea is correct or not.

(*c*) *Ploidy level*

Comparisons of diploid and polyploid angiosperms have shown that polyploids have shorter meiotic divisions than diploid species with corresponding DNA amounts. For instance, the duration of meiosis in hexaploid *Triticum aestivum* (24 h) is much shorter than in diploid *Allium cepa* (96 h) although both species have very similar nuclear DNA contents (Bennett 1972). Furthermore, comparison of the meiotic times for polyploid and related or parent diploid cereal species (table 1) shows that all the polyploid species have much shorter meiotic times than do their related diploid species (Bennett & Smith 1972; Finch & Bennett 1972).

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In a series of related polyploids the departure from the meiotic duration for a diploid increased with increasing ploidy level. Thus, the tetraploid showed the least difference, the hexaploid an intermediate difference, and an octoploid the greatest difference from the related diploid species (Bennett & Smith 1972). This effect of ploidy level (figure 5) has been found for both allo- and autopolyploids, and in polyhaploids (Bennett, Dover & Riley 1974). For instance, the duration of meiosis was 39 h in autotetraploid, and 51 h in diploid *Secale cereale*, while it was 31 h in the autotetraploid and 39 h in the diploid Ymer variety of *Hordeum vulgare* (Finch & Bennett 1972). In the natural allopolyploid wheat series meiosis lasted 42 h in the diploid *Triticum monococcum*, 30 h in the tetraploid *T. dicoccum*, and only 24 h in two varieties of *T. aestivum* which is a hexaploid. In a polyploid hybrid containing 21 *T. aestivum* chromosomes and 7 *S. cereale* chromosomes the duration of meiosis, in the almost total absence of chromosome pairing, was about 35 h which is shorter than in either diploid wheat or rye species and intermediate between

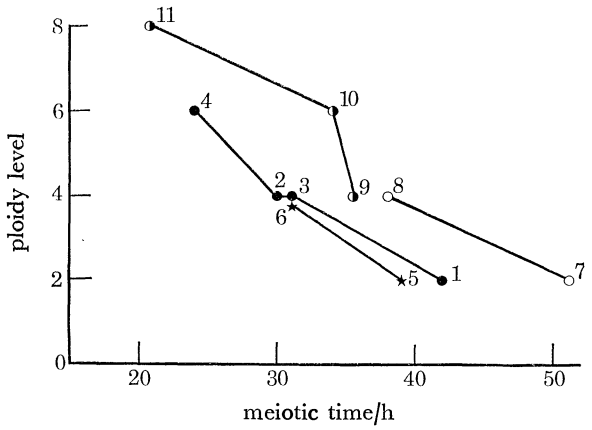

FIGURE 5. The relation between duration of meiosis and ploidy level in wheat (●), barley (★), rye (○) and wheat–rye hybrids (◑). Key to points: 1, *Triticum monococcum*; 2, *T. turgidum* var. *durum*; 3, *T. dicoccum*; 4, *T. aestivum* cv. Chinese Spring; 5, *Hordeum vulgare* cv. Ymer; 6, *H. vulgare* cv. Ymer (autotetraploid); 7, *Secale cereale* cv. Petkus Spring; 8, *S. cereale* cv. Svalov 4×; 9, *Triticum aestivum* × *Secale cereale* ($2n = 28$); 10, *Triticale* cv. Rosner; 11, *Triticale* (Chinese Spring × King II) amphidiploid.

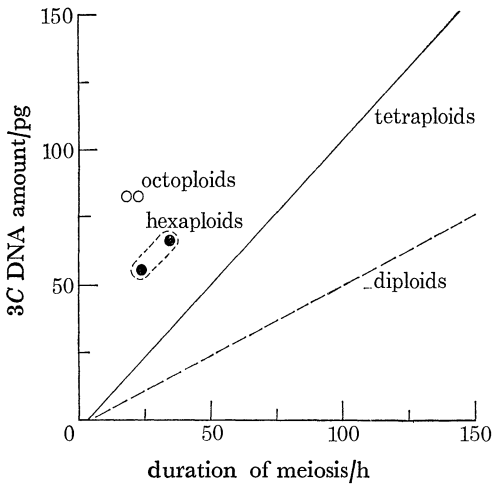

FIGURE 6. The relation between nuclear DNA amount and the duration of meiosis for diploids (broken regression line), tetraploids (unbroken regression line) hexaploids (●) and octoploids (○).

the estimates for tetraploid *T. dicoccum* (30 h) and tetraploid *S. cereale* (38 h). The effect of polyploidy giving faster meiosis is also seen in new amphidiploids. Thus, in *Triticale* (a synthetic amphiploid between *T. aestivum* and *S. cereale*) the meiotic time in two octoploids (table 1) was much faster than in their related parent species (Bennett & Smith 1972).

The effect of increasing ploidy level in reducing the duration of meiosis apparently contradicts the relation between nuclear DNA content and meiotic duration described above, since, the cereal polyploids studied all have higher DNA amounts and shorter meiotic divisions than their related diploids. This apparent contradiction was in part resolved when it was shown (Bennett 1973*a*) that there is a significant positive relation between DNA amount and the duration of meiosis for tetraploids whose slope ($b = 1.07 \pm 0.13$) is about twice that for diploids ($b = 0.50 \pm 0.03$). The magnitude of the departure of results for polyploid cereals from the regression line for nuclear DNA content on meiotic duration for diploids increases with increasing ploidy level (figure 6). It seems reasonable to suggest, therefore, that (if these results are typical for angiosperms) there is a significant positive correlation between nuclear DNA content and meiotic duration for species at each ploidy level, but that the slope of the regression increases with increasing ploidy level.

(*d*) *The genotype*

Genotypic control of meiotic chromosome behaviour is well known (Rees 1961) and control of pairing by variation in the duration of pairing was postulated by Darlington (1940) in his time-limit for pairing hypothesis. Nevertheless, only two examples of genetic control of the duration of meiosis are known. Klein (1972) stated that the duration of meiosis was increased in two *Pisum sativum* mutants, compared with normal plants. However, this claim, which may well be correct, is based only upon correlations between anther length and meiotic stage and not on direct measurements of the rate of meiotic development.

Experiments to screen for variation in meiotic time have been carried out using the wide range of genetic variation available in *Triticum aestivum* (Bennett & Smith 1974; Bennett *et al.* 1974). Meiosis was timed in nullisomic, tetrasomic, ditelocentric, substitution, addition and mutant lines of the variety 'Chinese Spring'. It was found that individual chromosomes differ in their effects on the rate of meiotic development. Thus, the absence of chromosome 5B had a large effect on slowing down development while the absence of chromosome 7B had no detectable effect. It was shown that the gene(s) responsible for the effect on meiotic time on chromosome 5B are located on the short arm; however, the mechanism responsible for the effect is unknown. It was noted that while the removal of chromosome 5B resulted in a decreased rate of meiotic development, the addition of extra 'doses' of this chromosome did not produce any detectable increased rate of meiotic development above that found in euploid plants. These results might be expected since the removal of any chromosome bearing genes controlling any meiotic event would upset the balance of the delicate meiotic control mechanism and result in a less efficient meiotic division. At the same time it might be expected that proportional changes in the gene dosage involving many or all of the chromosomes controlling meiosis would be required before an increased efficiency in meiotic behaviour would be found. Polyploids have undergone such a change involving every gene on every chromosome so that meiosis is completed more rapidly.

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4. The nucleotype

The precise relation between nuclear DNA content and the duration of meiosis illustrated in figure 2 shows that the mass of DNA per nucleus plays a major role in determining the duration of meiosis. Meiosis in *Antirrhinum majus*, which has 5.5 pg DNA per cell, and in *Lilium longiflorum*, which has 106 pg, is similar in every respect. It consists of the same stages occurring in the same order; only the duration is different being about 24 h in *A. majus* and 192 h in *L. longiflorum*. Compared with *A. majus*, *L. longiflorum* need not include any new information in its extra DNA to undergo meiosis and its longer meiotic time may result from the increased mass of nuclear DNA to be organized during the division. It has been suggested (Bennett 1971), therefore, that DNA influences development in two ways. First, through its informational content (the genotype) it determines the available systems of enzymes and other molecules directly concerned with the regulation of development. Second, DNA can affect the rate of development indirectly, and independently of its informational content, apparently by the physical or mechanical consequences of its mass. It is necessary, therefore, to distinguish between two effects of DNA, the first depends upon nucleotide sequences that by appropriate transcription results either directly or indirectly in the production of functionally significant molecules. The second irrespective of its nucleotide sequences merely by its presence or absence modifies the speed of development. It was proposed (Bennett 1971), that the term 'nucleotype' should be used to describe the latter, as 'genotype' describes the former. The nucleotype is defined as that condition of the nucleus which affects the phenotype independently of the informational content of the DNA. Two questions arise, namely 'How does DNA amount affect the rate of meiotic development?' and indeed, 'Is it DNA amount which determines the rate of meiotic development?'

Nuclear DNA content has been shown to be directly proportional to many chromosomal, nuclear and cellular characters including their size, mass and rate of development (for a review see Bennett 1972, 1973*b*). For instance, chromosomal histone is directly proportional to nuclear DNA amount. Thus, other molecules in the nucleus besides DNA contribute to the nucleotype and presumably can affect the phenotype. While the nucleotype is probably determined by several nuclear characters, all of which may affect meiotic time, it is convenient to consider the nucleotypic effect of DNA amount alone, since this character probably has the predominant effect, and is probably causal in its relations with many other nuclear characters. Thus, presumably DNA amount has its effect on the rate of meiotic development through the complex of characters with which it is intimately related, which together constitute the nucleotype.

While DNA amount clearly exercises a major and precise effect on the duration of meiosis, nevertheless, it is not DNA amount *per se* which determine this effect, since for instance:

(i) Species with the same DNA amount but different ploidy levels have very different meiotic times.

(ii) Cells with nuclei of different ploidy levels in a p.m.c. mosaic complete meiosis at the same rate despite their having different nuclear DNA contents.

(iii) Comparisons of the cereal species which exhibit large effects of DNA amount and ploidy level on the duration of meiosis show little or no effect of these characters on the rate of nuclear development in young coenocytic endosperm, although, effects similar to those found at meiosis are seen once the endosperm becomes a cellular tissue (Bennett, Smith & Barclay 1975).

Expression of the nucleotype can apparently depend to a large degree on the cytoplasm. Heslop-Harrison (1966) has shown that p.m.cs within a single loculus form a syncytium during much of the meiotic cycle. Thus, while meiosis is shorter in polyploid nuclei than in diploid nuclei when these occur in separate species (see example (i) above), nevertheless, when nuclei with different ploidy levels occur together (see example (ii) above) they all complete meiosis at the same rate, determined by their common cytoplasm.

Clearly the observed duration of meiosis is the product of a complex genotype–nucleotype–environment interaction. In a constant external environment, variation in the plant genotype can modify the expression of the nucleotype, and vice versa. Variation in the genotype affects the rate of meiotic development by altering the internal plant environment (i.e. the nucleus or cytoplasm) in which the genotype has to function. Rather than considering the duration of meiosis as the product of a three way interaction, as above, it may be helpful to view the nucleotype as part of the environment in which the genotype has to function. Thus, variation in nuclear DNA content represents an intracellular environmental change.

TABLE 7. THE DURATION OF MALE AND FEMALE MEIOSIS IN SEVERAL HIGHER PLANT SPECIES GROWN AT 20 °C

species	ploidy level	duration of meiosis/h	
		in p.m.cs	in e.m.cs
1. *Hordeum vulgare* cv. Sultan	2×	39.4	43
2. *Tradescantia paludosa*	2×	126	c. 80
3. *Lilium* hybrid cv. Black Beauty	2×	252	384
4. *Triticum aestivum* cv. Chinese Spring	6×	24	26.2
5. *Triticale* cv. Rosner	6×	34	32.2
6. *Lilium* hybrid cv. Sonata	3×	180	252

The duration of female meiosis for species 1 and 4 are from Bennett, Finch, Smith & Rao (1973); for species 3 and 6 from Bennett & Stern (1975*a*), while those for species 2 and 5 were estimated by Bennett & Smith using the method described by Bennett *et al.* (1973), but have not been published previously.

5. FEMALE MEIOSIS

(*a*) *Plants*

As mentioned earlier, in species with two track heredity the duration of female meiosis has been estimated in far fewer species than male meiosis. However, reliable estimates for the duration of meiosis in embryo sac mother cells (e.m.cs) have been published for two cereal species (Bennett *et al.* 1973) and two *Lilium* hybrids (Bennett & Stern 1975*a*), and these together with times for two other species not published previously are given in table 7.

In many species (for instance, *Triticum aestivum*, *Hordeum vulgare* and *Triticale* cv. Rosner) male and female meiosis occurs on average synchronously within the same floret, while in many other species (for instance, *Lilium* cv. Black Beauty and cv. Sonata) female meiosis does not commence until male meiosis has been completed in the same floret. Thus, in *T. aestivum*, *H. vulgare* and *Triticale* cv. Rosner the duration of male and female meiosis is almost identical. However, in *Lilium* cv. Black Beauty and cv. Sonata female meiosis is about 50 % longer than male meiosis (Bennett & Stern 1974*a*). Interestingly, in *Lilium* the e.m.c. is much larger than the p.m.c. at the same stage of meiosis and the mean chiasma frequency is higher in e.m.cs than in p.m.cs

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(Fogwill 1958), while in the three cereal species listed in table 7 both the volumes of the two types of meiocyte and their chiasma frequencies, are approximately the same (Bennett *et al.* 1973). These data are compatible with Darlington's time-limit for pairing hypothesis. However, it remains possible that the increased chiasma frequency in *Lilium* e.m.cs (Fogwill 1958) is caused by the larger volume of the female meiocyte rather than by the increased duration of zygotene and pachytene in e.m.cs.

Comparison of data for the six angiosperm species listed in table 7 shows that, despite the variation noted above, there is a highly significant relationship ($P < 0.001$; $r = 0.96$) between the duration of male and female meiosis (figure 7). Consequently, it can be reasonably concluded that factors (e.g. nuclear DNA content and ploidy level) which determine the duration of male meiosis are also important and effective in determining the duration of female meiosis.

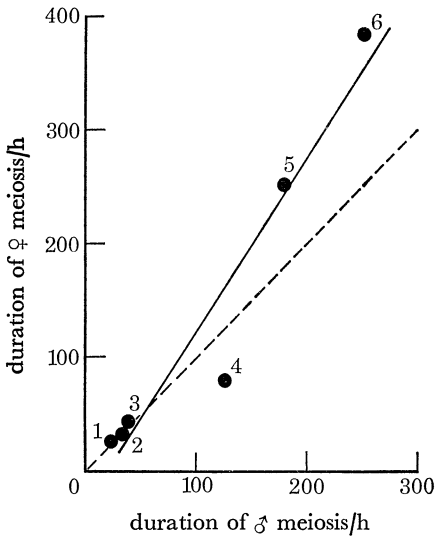

FIGURE 7. The relationship between the duration of male meiosis and the duration of female meiosis. The solid line is the regression line for the duration of female meiosis on male meiosis for the six angiosperm species listed in table 7 grown at 20 °C ($P < 0.001$; $r = 0.96$), while the broken line is the expected regression line assuming the durations of male and female meiosis are always identical in a given species.

(*b*) *Animals*

Estimates of the duration of female meiosis have been made for *Drosophila melanogaster* (Grell & Chandley 1965; Chandley 1968), *Xenopus laevis* (Bird & Birnstiel 1971; Coggins & Gall 1972), *Mus musculus* (Lima-de-Faria & Borum 1962; Crone, Levy & Peters 1965) and *Oryctolagus* (Kennelly, Foote & Jones 1970); also for the post-dictyate stages in *Homo sapiens* (Edwards 1965).

In each case where data are available for both sexes, the duration of meiosis is greatly prolonged in the female compared with the male. The extra duration of female meiosis is often the result of developmental holds (for instance, the long period spent at pachytene in *Xenopus laevis*, and the long period in the dictyate condition at diplotene in mammals). Many conclusions regarding the time and duration of male meiosis apply equally to female meiosis despite its extra duration. For instance, the rate of development during female meiosis is much slower than in somatic meristematic cells, and the duration of first meiotic prophase is very long compared with the stages from first metaphase to second telophase.

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Apparently the relative durations of the stages of first prophase prior to the resting stage in female meiosis of mammals may differ markedly from their durations in male meiosis of the same species. Thus, the duration of leptotene in male *Mus musculus* was 2–3 days (Ghosal & Mukherjee 1971), while in female *M. musculus* it was only 3–6 h (Crone, Levy & Peters 1965). Similarly, the combined durations of leptotene, zygotene, and pachytene in male *Mus musculus* was about 10 days (Kofman-Alfaro & Chandley 1970) while in females their combined duration totalled only about 4 days (Lima-de-Faria & Borum 1962). However, the duration of pre-dictyate stages of meiosis in *Oryctolagus* was about 12 days (Kennelly *et al.* 1970), which is probably not much shorter than the duration of corresponding development during male meiosis for this species (Swierstra & Foote 1965).

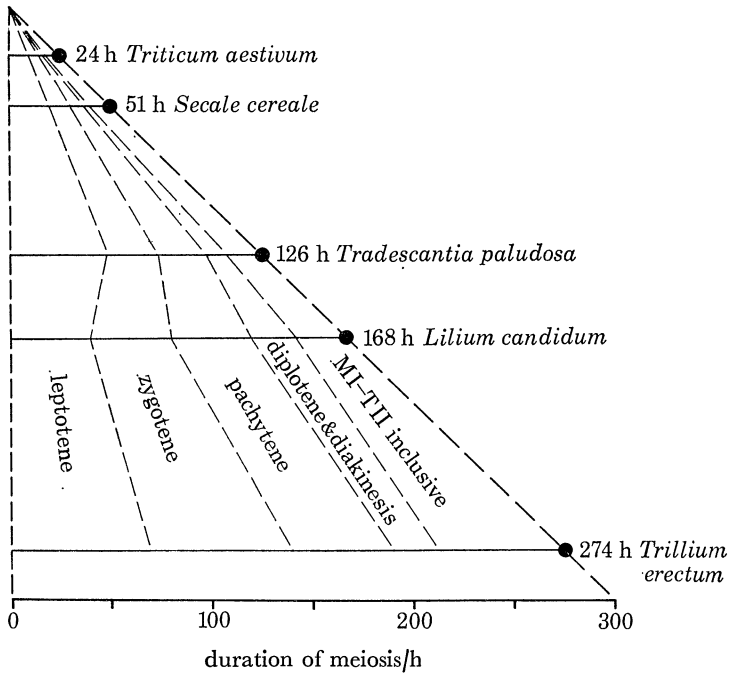

FIGURE 8. Illustration showing that increasing the duration of meiosis in angiosperms generally results from proportional increases in all the stages of meiosis.

6. PROPORTIONALITY

With the obvious exception of increased meiotic duration caused by developmental holds, changes in the duration of meiosis in higher plants usually result from proportional alterations of all the stages (figure 8) rather than large changes in just one or a few. This is true irrespective of whether the change in meiotic duration results from variation in temperature (Bennett, Smith & Kemble 1972), DNA amount (Bennett 1971, 1973), ploidy level (Bennett & Smith 1972) or from its occurrence in male and female meiocytes (Bennett & Stern 1975*a*). Thus, in higher plants the stages of meiosis generally occupy relatively constant proportions of the time spent in the division. Nevertheless, some variation in this character in plants has been noted. For instance, zygotene and pachytene together occupy about 40 % of the total meiotic time in diploid and tetraploid *Secale cereale*, but only about 23 % in hexaploid wheat. The possible importance

of this difference for the pairing of rye chromosomes in wheat–rye amphidiploid (*Triticale*) has been noted (Bennett & Kaltsikes 1973). Thus, chromosome pairing is much lower in octoploid *Triticale* (in which zygotene and pachytene together occupy about 25 % of the meiotic time) than in a hexaploid *Triticale* where the proportion of meiosis occupied by zygotene and pachytene (40 %) is similar to that found in rye.

While data for animal species show a strong tendency for changes in the duration of meiosis to result from proportional changes in the duration of all its stages, variation in the proportion of meiosis taken by individual meiotic stages is clearly much greater between animal species than has been noted between angiosperms. Moreover, there are obviously large differences between angiosperms and many animal species with respect to the relative proportions of the total meiotic time taken by individual stages or groups of stages. For example, in angiosperms the longest stage of male meiosis is leptotene (Bennett 1971), but in *Triturus vulgaris* it is zygotene (Callan & Taylor 1968) while in *Mus musculus*, *Cricetulus griseus*, *Mesocrecetus auratus* and *Homo sapiens* it is pachytene (Utakoji 1966; Lima-de-Faria *et al.* 1968; Ghosal & Mukherjee 1971). Similarly, in angiosperms pachytene usually occupies about 20 ± 5 % of the total meiotic time. However, in male *Triturus vulgaris* pachytene occupied about 25 % of the total meiotic time (Callan & Taylor 1968) while in *Cricetulus griseus* it occupied about 75 % (Utakoji 1966). Similarly, in angiosperms the inclusive durations of the stages of meiosis after diakinesis usually occupy about 30 ± 5 % of the total meiosis time, but in *Triturus vulgaris* (Callan & Taylor 1968) and *Mus musculus* (Ghosal & Mukherjee 1971) these stages occupied only about 8 %, and 5 %, respectively, of the total meiotic time.

The constant proportionality of stages noted for meiosis in plants has been shown to apply to premeiotic and post-meiotic stages also (Bennett & Smith 1972; Bennett *et al.* 1974). For instance, there is a highly significant correlation between the duration of meiosis and the duration of pollen development in cereal species (Bennett & Smith 1972). The importance of such correlations and the relation between nuclear DNA content and minimum generation time in plants has been considered elsewhere (Bennett 1972, 1973).

7. Wider implications of meiotic duration

The duration of meiosis often has much wider implications for the organism than those affecting the meiotic process *per se*. For instance, at 20 °C the duration of meiosis in some *Fritillaria* species is probably about 3–4 weeks (Barber 1942) while other ephemeral species can complete a life cycle in about the same time. Short meiosis is, therefore, an essential adaptive feature for all species with an ephemeral life cycle. As short meiosis and low DNA amount are correlated, ephemeral species have both (Bennett 1972). A corollary is that species with very high DNA amounts cannot display the ephemeral life-cycle type. No exception to this expectation has been noted.

Short meiosis is also an essential adaptation for biennial and perennial species which complete meiosis and other stages of reproductive development during a very short growing season (for instance, many arctic, alpine and desert species). An intriguing adaptation related to the need for rapid meiotic development was reported for the high arctic plant *Dryas integrifolia* growing at 82 °N in Canada (Kevan 1975). This species has heliotropic flowers whose corollas focus heat on the sporophylls, thereby raising their temperature above ambient by up to 8 °C. Assuming a Q_{10} of at least 2.3 under arctic summer conditions, this temperature increase would increase the

rate of meiotic development to twice that which would occur if meiosis occurred at ambient temperatures.

Because high nuclear DNA amount is related to slow rate of development at many stages of the life cycle besides meiosis, there is a relation between nuclear DNA amount and minimum generation time in higher plants (Bennett 1972, 1973*b*) and probably in other organisms. Consequently, there is a close correlation between long meiotic divisions under temperate conditions and the perennial life-cycle type. Many perennial species with high DNA amounts complete meiosis in their perennating organs outside the season of active growth, e.g. *Hyacinth* sp., *Endymion nonscriptus*, *Trillium erectum*. This behaviour is of adaptive significance since it allows the species to make the maximum use of the growing season for either vegetative growth or post-meiotic stages of reproductive and seed development. The adaptation is especially useful for species with high DNA amounts which grow in extreme environments with very short growing seasons and low mean temperatures, for example, in *Fritillaria aurea* which grows in Greece at altitudes of about 2000 m and has an active growing season of only 3 or 4 weeks between the thawing of the snows and the onset of severe drought.

It is concluded, first, that the duration of meiosis itself can limit the type of life cycle which a species can display; and second, that in many species the duration of meiosis is an essential adaptive feature suited to its life-cycle type in its normal environment. The examples cited above are all for plants, but similar relationships must also apply for animals. For example, *Drosophila* under ideal conditions can complete a life cycle in about 12 days while several grasshoppers take longer than this to complete male meiosis (table 2).

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Discussion

K. R. Lewis (*Department of Botany, University of Oxford*). I would like to ask Dr Bennett whether he has any information on cycle time in polytene or endopolyploid nuclei as they proceed to higher DNA values? These would seem to be suitable situations for studying the combined effects of DNA amounts and ploidy.

M. D. Bennett. To my knowledge there is very little detailed knowledge regarding cycle times in polytene or endopolyploid nuclei as they proceed to higher DNA values. There is some data for *Drosophila melanogaster* embryos (Rudkin 1969) and *Calliphora erythrocephala* (Pearson 1974) in animals, and for *Bryonia dioica* (Barlow 1975) in a higher plant. However, the example with which I am most familiar concerns the development of antipodal cell nuclei in the embryo sac of *Triticum aestivum* cv. Chinese Spring (Bennett *et al.* 1973). Here the embryo sac contains three haploid (1*C*–2*C*) antipodal nuclei 120 h before anther dehiscence and self-pollination. By dehiscence the embryo sac contains up to 30 antipodal cells, some of which contain nuclei with up to 256*C* DNA amounts. It has been shown that the cycle times during endoreduplication in these antipodal cells do not exceed 15 h and may be as short as 12 h. The cell cycle time in root-tip meristem cells of this cultivar grown at the same temperature (20 °C) is about 12.5 h. It seems reasonable to conclude, therefore, that in this example at least there is no great change in cycle time accompanying the movement to higher DNA values. I believe the results for *Calliphora* lead to the same conclusion as do those for Bryonia (Barlow 1975).

References

Barlow, P. W. 1975 The polytene nucleus of the giant hair cell of *Bryonia* anthers. *Protoplasma* **83**, 339–349.
Bennett, M. D., Rao, M. K., Smith, J. B. & Bayliss, M. W. 1973 Cell development in the anther, the ovule, and the young seed of *Triticum aestivum* L. var Chinese Spring. *Phil. Trans. Roy. Soc. Lond.* B **266**, 39–81.
Pearson, M. J. 1974 The abdominal epidermis of *Calliphora erythrocephala* (Diptera) I. Polyteny and growth in the larval cells. *J. Cell Sci.* **16**, 113–131.
Rudkin, G. T. 1969 Non replicating DNA in *Drosophila*. *Genetics Suppl.* **61**, 227–328.

D. J. Harberd (*University of Leeds*). I wonder if Dr Bennett would comment on a curious anomaly in the figures he has given for the duration of meiosis in the different wheat lines. Quite clearly the nulli 5B no longer behaves in the manner typical of hexaploids. But it must be coincidental that the duration is similar to that of tetraploid species since the nulli 5B cannot have a DNA content similar to that of tetraploids, but presumably some 40 % more. 30 h fits in fact neither with the hexaploid nor with the tetraploid DNA/duration regression lines.

M. D. Bennett. In fact nulli 5B-tetra 5D has about 24 % more DNA than the tetraploid wheat *T. dicoccum*, rather than 40 % as suggested by Dr Harberd. (This is because the D-genome is the smallest of the three diploid genomes present in hexaploid wheat.) Nevertheless, Dr Harberd is correct in pointing out that the duration of meiosis for nulli 5B-tetra 5D does not fit exactly the expected time for either a tetraploid with as much DNA as nulli 5B-tetra 5D (about 37 h) or hexaploid *T. aestivum* (24 h). The observed time (30 ± 2 h) is too fast for the former and too slow for the latter. While the cause of the observed time in nulli 5B-tetra 5D is unknown, it is presumably the result of the interaction of its DNA amount and its genotype. The real anomaly is perhaps that meiosis is shorter in polyploids than in their parent diploids, but given that this is so it is presumably not the additional DNA but the additional complete balanced sets of genes

which make this possible. It may be only coincidental that the meiotic rates in nulli 5B-tetra 5D and tetraploid wheat are the same, but I do not accept this view. It seems likely to me that the base rate for meiosis is determined by the DNA amount per diploid genome. Any quickening of this rate is determined by the number of complete balanced set of genes per nucleus in excess of two (the number in a diploid). Thus, I believe that the rate observed in nulli 5B-tetra 5D is the same as that observed in a tetraploid wheat because both contain the same number of complete balanced sets of genes (namely 4).

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