Contribution du laboratoire de botanique de l'Université d'Utrecht.

Some numerical proportions in panmictic populations

by

L. BAAS BECKING.

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§ 1. Although by different authors several properties of the mendelian population are treated mathematically, there is still a great gap in the investigations.

A general and systematic treatment is lacking. Partially this is due to the fact that many investigators reject the use of formulas for living organisms, as nature probably never will follow a rigid scheme, whereas for the other part the imperfectness of our knowledge is the consequence of a certain lack of interest most biologists show for mathematical questions.

It is to be regretted that such a general theory does not exist. The different publications do not give a sufficient foundation for such a theory, being too heterogenous of method. Jennings (1916) does not give the derivation of his formulas. Wentworth & Remick (1916), Bruce (1917) and Robbins (1918) are using differential calculation, while Bone (Heukels 1915) obtains his formulas by means of the Gaussian theory of probabilities. None of the authors (Heukels exepted) consider a population with more than one mendelian factor. It is clear that the general theory must have the following qualities:

1°. The method must be homogenous;

2°. The theory must consider populations with an unlimited number of mendelian factors;

3°. All matings must be equally probable, in special cases (as for instance brother and sister mating, inbreeding, sex-linked inheritance etc.) certain combinations equal numerically to zero.

I have tried, with the help of simple arithmatics to deduce a formula for the numerical proportion that will exist in a population with p mendelian factors after n random matings.

I did obtain other formulas, but, failing in deducing them by means of simple arithmatics I do not give them here. For it seems to me desirable to explain always logically the forms given and not to use results of a mathematical process without giving its derivation, as for instance Jennings (1916) and Johannsen (1913) did with most of their forms.

§ 2. Proportions in a population with one mendelian factor.

Jennings (1916) treats this problem, considering a population consisting of R individuals AA, T indiv. aa and S indiv. Aa. He obtains the following results: if the constitution of any generation n is $RAA + Taa + SAa$ then the constitution of the next following generation will be $AA = (S + 2R)^2$; $aa = (S + 2T)^2$; $Aa = 2(S + 2R)(S + 2T)$. He has not been able to obtain a serviceable formula giving directly the proportions for any later generation, without working out the proportions for the intervening generations.

It is, however, a simple thing to deduce that formula. The proportions of AA; aa and Aa have the pecularity to remain $(S + 2R)^2 : (S + 2T)^2 : 2(S + 2R)(S + 2T)$.

Jennings (1916) admits in a correctionslip in the reprints of his article that the formula is of general importance, but does not give a derivation.

This has been done by Wentworth & Remick (1916) but with the help of differential calculation. Therefore I will give that derivation in a more simple way, that will run as follows:

The population consists of RAA, Taa, SAa and gives gametes in a mumber 2RA, 2Ta, SA and Sa, or totally: $(S + 2R)A : (S + 2T)a$.

Combination of the gametes gives in the next following generation: $(S+2R)^2AA$, $(S+2T)^2aa$; $2(S+2R)(S+2T)Aa$. How are the proportions in the F_2, considering that there is random mating?

$$\text{Let}\quad \left.\begin{array}{r} (S + 2R)^2 \text{ equal } V \\ (S + 2T)^2 \text{ equal } W \\ 2(S+2R)(S+2T) \text{ equal } X \end{array}\right\} \quad \text{and we will have the}$$

following equation:

$$(X + 2V)^2AA;\quad (X + 2W)^2aa;\quad 2(X + 2V)(X + 2W)Aa.$$

If we substitute the values of S, R and T in this equation, we will get:

$$\begin{array}{l} \{2(S + 2R)(S + 2T) + 2(S + 2R)^2\}^2AA; \\ \{2(S + 2R)(S + 2T) + 2(S + 2T)^2\}^2aa; \\ 2\{2(S + 2R)(S + 2T) + 2(S + 2R)\} \\ \{2(S + 2R)(S + 2T) + 2(S + 2T)\}Aa \end{array}$$

or,

$$\begin{array}{l} 2^4(S + 2R)^2(S + R + T)^2AA; \\ 2^4(S + 2T)^2(S + R + T)^2aa; \\ 2^5(S + 2R)(S + 2T)(S + R + T)^2Aa. \end{array}$$

The same method worked out for several other generations gives for the:

$$F_3\quad \left.\begin{array}{l} 2^{12}(S + 2R)^2(S + R + T)^6AA \\ 2^{12}(S + 2T)^2(S + R + T)^6aa \\ 2^{13}(S + 2R)(S + 2T)(S + R + T)^6Aa \end{array}\right\}$$

$$F_7 \quad \left.\begin{aligned} &2^{252}(S+2R)^2(S+R+T)^{126}AA \\ &2^{252}(S+2T)^2(S+R+T)^{126}aa \\ &2^{253}(S+2R)(S+2T)(S+R+T)^{126}Aa \end{aligned}\right\}$$

$$F_{10} \quad \left.\begin{aligned} &2^{2044}(S+2R)^2(S+R+T)^{1022}AA \\ &2^{2044}(S+2T)^2(S+R+T)^{1022}aa \\ &2^{2045}(S+2R)(S+2T)(S+R+T)^{1022}Aa \end{aligned}\right\}$$

we can conclude directly that the proportions in the F_n generation will be

$$\left.\begin{aligned} &2^{2y}(S+2R)^2(S+R+T)^yAA \\ &2^{2y}(S+2T)^2(S+R+T)^yaa \\ &2^{2y+1}(S+2R)(S+2T)(S+R+T)^yAa \end{aligned}\right\}$$

The relation between these forms is:

$(S+2R)^2 : (S+2T)^2 : 2(S+2R)(S+2T)$, for we can devide the forms by $2^{2y}(S+R+T)^y$. The relation remains constant in all generations. The general formula will run:

$$F_n \quad \left.\begin{aligned} &2^{(2^{n+1}-2^2)}(S+2R)^2(S+R+T)^{(2^n-2)}AA: \\ &2^{(2^{n+1}-2^2)}(S+2T)^2(S+R+T)^{(2^n-2)}aa: \\ &2^{(2^{n+1}-2^2+1)}(S+2R)(S+2T)(S+R+T)^{(2^n-2)}Aa \end{aligned}\right\} \,..\,(I)$$

N.B. Wentworth & Remick (1916) give in their derivation of the formulas the following exponents for the factor 2: $4(2^{n-2}+2^{n-3}+\ldots\ldots+2^{n-n})$. I obtained this form too, but, finding the more practical form $(2^{n+1}-2^2)$ by summation, I rejected the first one. Karl Pearson (1909) has used the derived formula already. He remarks (l. c. pg. 223): „the stability after the first generation is very obvious, but, as far as I know, was first stated in print by G. H. Hardy (1908)".

Therefore it is surprising that neither Jennings nor Wentworth were acquainted with these forms.

An example from experimental genetics will illustrate the use of the formula. Erwin Baur (1914) considers the case that a population of mice originates from six parents: 2 ♂ AA; 2 ♀ AA; 1 ♂ Aa; 1 ♀ Aa; all matings are equally probable.

The constitution of the F_1 will be: . . . . . (I)

$$AA = (S + 2R)^2 = (1 + 2 \,.\, 2)^2 = 25:$$
$$aa = (S + 2T)^2 = (1 + 2 \,.\, 0)^2 = 1:$$
$$Aa = 2(S + 2R)(S + 2T) = 2 \,.\, 1 \,.\, 5 = 10.$$

Baur obtains the same results by writing out all possible combinations. He remarks that the proportion will remain the same if there is always random mating; however without proving it. The proof can be deduced immediately from form (I).

If the parental generation is $pAA + qAa + paa$, then R will be T, and in the filial generation the proportion AA : Aa : aa = 1 : 2 : 1 will exist. *This proportion remains constant,* for the homozygotes are again numerically the same. In populations with more mendelian factors we shall obtain similar results.

§ 3. Proportions in a population with two mendelian factors.

The population consists of:

gametes:	AABB	AABb	AAbb	AaBB	AaBb	Aabb	aaBB	aaBb	aabb
quantities:	m	n	o	p	q	r	s	t	u
AB	$2m$	n		p	$\frac{1}{2}q$				
Ab		n	$2o$		$\frac{1}{2}q$	r			
aB				p	$\frac{1}{2}q$		$2s$	t	
ab					$\frac{1}{2}q$	r		t	$2u$

Or, totally, there will be

$$\left.\begin{array}{lll} (2m + n + p + \frac{1}{2}q) & \text{of the gamete} & AB = M \times AB; \\ (2o + n + r + \frac{1}{2}q) & „ \quad „ \quad „ & Ab = O \times Ab; \\ (2s + p + t + \frac{1}{2}q) & „ \quad „ \quad „ & aB = S \times aB; \\ (2u + r + t + \frac{1}{2}q) & „ \quad „ \quad „ & ab = V \times ab. \end{array}\right\}$$

Mating at random will give the following number of individuals in the filial generation

$$\begin{array}{ll} \text{1) Homozygotes} & \left\{\begin{array}{l} M^2 \; AABB \\ O^2 \; AAbb \\ S^2 \; aaBB \\ V^2 \; aabb \end{array}\right. \\ \text{2) Heterozygotes} & \left\{\begin{array}{l} 2MO \; AABb \\ 2MS \; AaBB \\ 2(MV + OS) \; AaBb \\ 2OV \; Aabb \\ 2SV \; aaBb \end{array}\right. \end{array}$$

There exists the following relation between the F_n and F_{n+1}:

	F_n	F_{n+1}
AABB	m	$(2m + n + p + \frac{1}{2}q)^2$
AABb	n	$2(2m + n + p + \frac{1}{2}q)(2o + n + r + \frac{1}{2}q)$
AAbb	o	$(2o + n + r + \frac{1}{2}q)^2$
AaBB	p	$2(2m + n + p + \frac{1}{2}q)(2s + p + t + \frac{1}{2}q)$
AaBb	q	$2(2m + n + p + \frac{1}{2}q)(2u + r + t + \frac{1}{2}q) + 2(2o + n + r + \frac{1}{2}q)(2s + p + t + \frac{1}{2}q)$
Aabb	r	$2(2o + n + r + \frac{1}{2}q)(2s + r + t + \frac{1}{2}p)$
aaBB	s	$(2s + p + t + \frac{1}{2}q)^2$
aaBb	t	$2(2s + p + t + \frac{1}{2}q)(2u + r + t + \frac{1}{2}q)$
aabb	u	$(2u + r + t + \frac{1}{2}q)^2$.

In the F_{n+2} generation we will have:

$$m_{n+2} = (2m_{n+1} + n_{n+1} + p_{n+1} + \tfrac{1}{2}q_{n+1})^2, \text{ or}$$

$$m_{n+2} = (2M^2 + 2MO + 2MS + MV + OS)^2$$

$$m_{n+2} = \{M(M + O + S + V) + (M + O)(M + S)\}^2,$$

or, if $M + O + S + V$ equals Ψ

$$m_{n+2} = \{M\Psi + (M + O)(M + S)\}^2.$$

Following the same method we can find out the formulas for the other groups of individuals. The result is:

$$o_{n+2} = \{O\Psi + (M + O)(O + V)\}^2$$
$$s_{n+2} = \{S\Psi + (S + M)(S + V)\}^2$$
$$v_{n+2} = \{V\Psi + (V + O)(V + S)\}^2$$
$$n_{n+2} = 2\{M\Psi + (M+O)(M+S)\}\{O\Psi + (M+O)(O+V)\}$$
$$p_{n+2} = 2\{M\Psi + (M+O)(M+S)\}\{S\Psi + (S+M)(S+V)\}$$
$$r_{n+2} = 2\{O\Psi + (O+M)(O+V)\}\{V\Psi + (V+O)(V+S)\}$$
$$t_{n+2} = 2\{S\Psi + (S+M)(S+V)\}\{V\Psi + (V+O)(V+S)\}$$
$$q_{n+2} = 2\{M\Psi + (M+O)(M+S)\}\{V\Psi + (V+O)(V+S)\} + 2\{O\Psi + (O+M)(O+V)\}\{S\Psi + (S+M)(S+V)\}.$$

In the F_{n+3} generation we will have again:

$m_{n+3} = (2m_{n+2} + n_{n+2} + p_{n+2} + \frac{1}{2}q_{n+2})^2$ or, by substitution; $= [\{M\Psi + (M + O)(M + S)\}\{2\Psi^2\} + 2(M + S)\Psi \times 2(M + O)\Psi]^2$

$$= [2M\Psi^3 + 6\Psi^2(M + O)(M + S)]^2$$
$$m_{n+3} = 2^2\Psi^4\{M\Psi + 3(M + O)(M + S)\}^2.$$

N.B. If we write the above formula:

$$m_{n+3} = 2^2\Psi^6\left\{M + 3 \, . \, \frac{(M + O)(M + S)}{\Psi}\right\}^2$$ it is comparable with the forms found for m_{n+2} and m_{n+1}. They will run as follows:

$$m_{n+1} = 2^0\Psi^2\left\{M + 1 \, . \, \frac{(M + O)(M + S)}{\Psi}\right\}^2$$
$$m_{n+1} = 2^0\Psi^0\left\{M + 0 \, . \, \frac{(M + O)(M + S)}{\Psi}\right\}^2.$$

By the same method we can derive m_{n+4} (F_4) etc.

$$F_1 \quad 2^0 \, . \, \Psi^0\left\{M + 0 \, . \, \frac{(M + O)(M + S)}{\Psi}\right\}^2$$
$$F_2 \quad 2^0 \, . \, \Psi^2\left\{M + 1 \, . \, \frac{(M + O)(M + S)}{\Psi}\right\}^2$$
$$F_3 \quad 2^2 \, . \, \Psi^6\left\{M + 3 \, . \, \frac{(M + O)(M + S)}{\Psi}\right\}^2$$
$$F_4 \quad 2^8 \, . \, \Psi^{14}\left\{M + 7 \, . \, \frac{(M + O)(M + S)}{\Psi}\right\}^2$$

$$F_5 \quad 2^{22} . \Psi^{30}\left\{M + 15 . \frac{(M+O)(M+S)}{\Psi}\right\}^2$$

$$F_7 \quad 2^{114} . \Psi^{126}\left\{M + 63 . \frac{(M+O)(M+S)}{\Psi}\right\}^2$$

$$F_9 \quad 2^{494} . \Psi^{510}\left\{M + 255 . \frac{(M+O)(M+S)}{\Psi}\right\}^2$$

$$F_{10} \quad 2^{1004} . \Psi^{1022}\left\{M + 511 . \frac{(M+O)(M+S)}{\Psi}\right\}^2$$

According to this, the general formula will run:

$$m_n = 2^{(2^n - n.2)} . \Psi^{(2^n-2)}\left\{M + (2^{n-1} - 1)\frac{(M+O)(M+S)}{\Psi}\right\}^2 \text{(II)}$$

The numbers of the other groups are found by the same method.

What will be, for instance, the number of n_6?

$$n_6 = 2\sqrt{m_6 o_6}, \text{ or}$$

$$n_6 = 2 . 2^{(2^6-6.2)}\Psi^{(2^6-2)}\left\{M + (2^5-1)\frac{(M+O)(M+S)}{\Psi}\right\}$$
$$\left\{O + (2^5-1)\frac{(O+M)(O+V)}{\Psi}\right\}$$
$$= 2^{53}\Psi^{62}\left\{M + 31\frac{(M+O)(M+S)}{\Psi}\right\}$$
$$\left\{O + 31\frac{(O+M)(O+V)}{\Psi}\right\}$$

From the form (II) we can draw the conclusion that $\frac{m_n}{o_n} \lessgtr \frac{m_{n+1}}{o_{n+1}}$, or, *the population does not remain constant in its proportions*. This fact is in a great contrast with the results found in a population with one mendelian factor. I did'nt succeed in finding an author who has drawn attention to this contrast. This is due to the fact that in most of the cases, as I remarked above, the only population considered (Wentworth & Remick call it even the „generalised" population) is that with *one* mendelian factor.

§ 4. What qualities we can deduce from form (II)? In the first place we can ask: what will become of the proportions after perpetual panmixy in a great number of generations? Let us take f. i. the proportion $\frac{n}{m}$ after x generations:

$$\frac{n_x}{m_x} = 2\frac{2^{(2^x-2x)} \cdot \Psi^{(2^x-2)} \left\{ M + (2^{x-1}-1)\frac{(M+O)(M+S)}{\Psi} \right\} \left\{ O + (2^{x-1}-1)\frac{(M+O)(O+V)}{\Psi} \right\}}{2^{(2^x-2x)} \cdot \Psi^{(2^x-2)} \left\{ M + (2^{x-1}-1)\frac{(M+O)(M+S)}{\Psi} \right\}^2} =$$

$$= 2\frac{O + (2^{x-1}-1)\frac{(M+O)(O+V)}{\Psi}}{M + (2^{x-1}-1)\frac{(M+O)(M+S)}{\Psi}},$$

or, if we multiply by Ψ and divide by $(2^{x-1}-1)$:

$$\frac{n_x}{m_x} = 2\frac{\frac{O\Psi}{2^{x-1}-1} + (M+O)(O+V)}{\frac{M\Psi}{2^{x-1}-1} + (M+O)(M+S)}.$$

If we suppose x to be very great, the forms $\frac{O\Psi}{2^{x-1}-1}$ and $\frac{M\Psi}{2^{x-1}-1}$ will become very small, and can be neglected when x limits to ∞. So we find:

$\lim_{(x=\infty)} \cdot \frac{n_x}{m_x} = 2\frac{O+V}{M+S}$. The following values are easily derived:

$$\lim_{(x=\infty)} \frac{o_x}{m_x} = \frac{(O+V)^2}{(M+S)^2}; \quad \lim_{(x=\infty)} \frac{s_x}{m_x} = \frac{(S+V)^2}{(M+O)^2};$$

$$\lim_{(x=\infty)} \frac{p_x}{m_x} = 2\frac{S+V}{M+O}; \quad \lim_{(x=\infty)} \frac{t_x}{m_x} = 2\frac{(S+V)^2(V+O)}{(M+O)^2(M+S)}$$

$$\lim_{(x=\infty)} \frac{q_x}{m_x} = 4\frac{(V+O)(V+S)}{(M+O)(M+S)}; \quad \lim_{(x=\infty)} \frac{u_x}{m_x} = \frac{(V+O)^2(V+S)^2}{(M+O)^2(M+S)^2}.$$

If we make this forms homogenous we find for the F_∞:

$$m_\infty : n_\infty : o_\infty : p_\infty : q_\infty : r_\infty : s_\infty : t_\infty : u_\infty =$$
$$(M : O)^2 (M + S)^2 : 2(M + O)^2 (M + S) (O + V) :$$
$$(M + O)^2 (O + V)^2 : 2(M + O) (M + S)^2 (S + V) :$$
$$4(M + O) (M + S) (O + V) (S + V) :$$
$$2(M + O) (O + V)^2 (S + V) : (M + S)^2 (S + V)^2 :$$
$$2(M + S) (S + V)^2 (O + V) : (O + V)^2 (S + V)^2 . . \text{(III)}.$$

In this form $m_\infty u_\infty = (M + O)^2 (M + S)^2 (O + V)^2 (S + V)^2$
$o_\infty s_\infty = (M + O)^2 (O + V)^2 (M + S)^2 (S + V)^2$,
thus $m_\infty u_\infty$ and $o_\infty s_\infty$ being equal we conclude that $m_\infty : o_\infty = s_\infty : u_\infty$, or in words:

After a great number of panmictic matings there will exist a certain constant proportion between the numbers of two homozygotes.

If we take for instance the following population:

$$m : n : o : p : q : r : s : t : u =$$
$$1 : 3 : 1 : 2 : 2 : 2 : 3 : 1 : 1.$$

This population gives in the F_∞ (III)

$$81 : 252 : 156 : 162 : 504 : 392 : 81 : 252 : 156,$$

the proportion $\frac{m_\infty}{o_\infty} = \frac{s_\infty}{u_\infty}$.

§ 5. We can put the following question. Which are the proportions in a population that will remain constant in its composition? In other words; *the composition of the invariable population.* In such a population the proportion between two quantities remains constant, thus:

$$\frac{M^2}{O^2} = \frac{\left\{M + (2^{n-1} - 1) \frac{(M + O)(M + S)}{\Psi}\right\}^2}{\left\{O + (2^{n-1} - 1) \frac{(M + O)(O + V)}{\Psi}\right\}^2} \text{ or}$$

$$\frac{M}{O} = \frac{M + (2^{n-1} - 1) \frac{(M + O)(M + S)}{\Psi}}{O + (2^{n-1} - 1) \frac{(M + O)(O + V)}{\Psi}}$$

$$MO+(2^{n-1}-1)\frac{(M+O)(O+V)}{\Psi}M=MO+(2^{n-1}-1)\frac{(M+O)(M+S)}{\Psi}O$$

$$M(+O)(O+V)M=(M+O)(M+S)O$$

$$\therefore MO+MV=MO+OS \text{ or}$$

$$MV=OS.$$

If we take another quotient, f. i. $\frac{M^2}{2MO}$, or $\frac{m_n}{u_n}$, we always will find the same result $MV = OS$, or $\frac{M^2}{O^2}=\frac{S^2}{V^2}$.

[N.B. The derivation will run as follows: $\frac{m_n}{u_n} = c$, so

$$\frac{M+(2^{n-1}-1)\frac{(M+O)(M+S)}{\Psi}}{V+(2^{n-1}-1)\frac{(V+O)(V+S)}{\Psi}}=\frac{M}{V}$$

$$(M+O)(M+S)V=(V+S)(V+O)M, \text{ or}$$

$$M^2V+OMV+SMV+OSV=$$

$$V^2M+VSM+VOM+OSM.$$

$$M^2O+OSV=V^2M+OSM$$

$MV(M+V) = OS(M+V)$ or $MV = OS$]. In words:

If in a population the numbers of the homozygotes are proportional to each other in pairs, the population will remain *constant in its constitution*.

Every population attains that proportionality of the homozygotes (§ 4) after a great number of matings.

§ 6. *a*) The constitution of the population, which after a great number of generations will form all its homozygotes in equal number can be derived considering that

$$(M+O)^2(M+S)^2=(M+O)^2(O+V)^2=(M+S)^2(S+V)^2=(O+V)^2(S+V)^2$$

$$(M+O)(M+S)=(M+O)(O+V)=(M+S)(S+V)=(O+V)(S+V)$$

$$(M+O)(M+S)=(O+V)(M+O) \quad (M+O)(M+S)=(M+S)(S+V)$$

$$M+S=O+V\ \ldots\ (a) \qquad M+O=S+V\ \ldots\ (b)$$

(*a*) — (*b*) will be $S - O = O - S$, or $O = S$, if we substitute this result in form (*a*) we get $M = V$ or

$O^2 = S^2$; $M^2 = S^2$. These are the conditions for the P_1 generation. In words:

If in a population the numbers of the homozygotes are equal in pairs, then all the homozygotes will equal each other after a great number of generations.

b) If in a population the numbers of the homozygotes are all equal, the number of the diheterozygotes : monoheterozygotes : homozygotes = 4 : 2 : 1.

$$M^2 = O^2 = S^2 = V^2, \text{ so}$$
$$M^2 : 2MO : O^2 = 1 : 2 : 1$$
$$M^2 : 2(MV + OS) : 2OV = 1 : 4 : 2 \text{ etc.}$$

In this new population the homozygotes are proportional in number, so the population is constant (§ 5).

§ 7. Three mendelian factors.

We indicate the groups by the following letters:

AABBCC by	m	AABBCc	v	AABBcc	u'
AaBBCC	n	AaBBCc	w	AaBBcc	t'
aaBBCC	o	aaBBCc	x	aaBBcc	s'
AABbCC	p	AABbCc	y	AABbcc	r'
AaBbCC	q	AaBbCc	z	AaBbcc	q'
aaBbCC	r	aaBbCc	y'	aaBbcc	p'
AAbbCC	s	AAbbCc	x'	AAbbcc	o'
AabbCC	t	AabbCc	w'	Aabbcc	n'
aabbCC	u	aabbCc	v'	aabbcc	m'

Calling the gamete ABC = M, we will have for the number of that gamete $M = 2m + n + p + v + \frac{1}{2}q + \frac{1}{2}w + \frac{1}{2}y + \frac{1}{4}z$. The homozygote AABBCC will have in the filial generation the number M^2. In the second filial generation we will have

$$m_{n+2} = \{2M^2 + 2MO + 2MS + 2MV' + MV + OS + MS' + OV' + MO' + SV' + \tfrac{1}{2}MM' + \tfrac{1}{2}OO' + \tfrac{1}{2}SS' + \tfrac{1}{2}VV'\},$$

using the same nomenclature as in § 3, or

$$m_{n+2}=\tfrac{1}{4}\{M\Psi+(M+V')(M+O+S+V)+(M+O)(M+O'+S+V')+(M+S)(M+O+S'+V')\}$$

The calculation for the next generation becomes rather complicated, the number of groups being 27.

By the method explained in § 3 I obtained for four generations the following results:

Number of the homozygote AABBCC.

$P_1 : m$
$F_1 : M^2$
$F_2 : \tfrac{1}{4}[M\Psi+(M+V')(M+O+S+V)+(M+O)(M+O'+S+V')+(M+S)(M+O+S'+V']^2,$

Let $(M+O+S+V)$ equal φ
„ $(M+O'+S+V')$ „ φ_{24}
„ $(M+O+S'+V')$ „ φ_{34} (the indices point to the accents), then the value for the m_{n+3} will be:

$$m_{n+3}=[M\Psi^3+3\Psi^2\{(M+V')\varphi+(M+O)\varphi_{24}+(M+S)\varphi_{34}\}+6\Psi.\varphi.\varphi_{24}\varphi_{34}]^2$$

$$m_{n+4}=2^{16}\Psi^{24}[M\Psi^3+15\Psi^2\{(M+V')\varphi+(M+O)\varphi_{24}+(M+S)\varphi_{34}\}+204.\Psi.\varphi.\varphi_{24}\varphi_{34}]^2$$

Here I stopped with the calculation, the formula suffices for our goal, the special coefficients being of no interest. We can deduce the forms for the other homozygotes, and we will get after generalising them:

$$\left\{\begin{aligned}
m_x &= 2^{\alpha}\Psi^{\beta}[M\Psi^3+\gamma\Psi^2\{(M+V')\varphi+(M+O)\varphi_{24}+(M+S)\varphi_{34}\}+\delta\Psi.\varphi.\varphi_{24}.\varphi_{34}]^2\\
o_x &= 2^{\alpha}\Psi^{\beta}[O\Psi^3+\gamma\Psi^2\{(O+S')\varphi+(O+V)\varphi_{34}+(O+M)\varphi_{13}\}+\delta\Psi.\varphi.\varphi_{13}.\varphi_{34}]^2\\
s_x &= 2^{\alpha}\Psi^{\beta}[S\Psi^3+\gamma\Psi^2\{(S+O')\varphi+(S+V)\varphi_{24}+(S+M)\varphi_{12}\}+\delta\Psi.\varphi.\varphi_{12}.\varphi_{24}]^2\\
u_x &= 2^{\alpha}\Psi^{\beta}[V\Psi^3+\gamma\Psi^2\{(V+M')\varphi+(V+O)\varphi_{12}+(V+S)\varphi_{13}\}+\delta\Psi\varphi.\varphi_{12}.\varphi_{13}]^2\\
m'_x &= 2^{\alpha}\Psi^{\beta}[M'\Psi^3+\gamma\Psi^2\{(M'+V)\varphi_{1234}+(M'+O')\varphi_{13}+(M'+S')\varphi_{12}\}+\delta\Psi\varphi_{1234}\varphi_{12}.\varphi_{13}]^2\\
o'_x &= 2^{\alpha}\Psi^{\beta}[O'\Psi^3+\gamma\Psi^2\{(S+O')\varphi_{1234}+(O'+V')\varphi_{12}+(O'+M')\varphi_{24}\}+\delta\Psi\varphi_{1234}\varphi_{12}.\varphi_{24}]^2\\
s'_x &= 2^{\alpha}\Psi^{\beta}[S'\Psi^3+\gamma\Psi^2\{(S'+O)\varphi_{1234}+(S'+V')\varphi_{13}+(S'+M')\varphi_{34}\}+\delta\Psi.\varphi_{1234}.\varphi_{13}.\varphi_{34}]^2\\
u'_x &= 2^{\alpha}\Psi^{\beta}[V'\Psi^3+\gamma\Psi^2\{(M+V')\varphi_{1234}+(V'+O')\varphi_{34}+(V'+S')\varphi_{24}\}+\delta\Psi\varphi_{1234}\varphi_{24}\varphi_{34}]^2
\end{aligned}\right. \qquad \ldots\ldots\ldots \text{(IV)}$$

We can treat this formula as an exact analogon of the form found in § 3.

In the first place I derived the limit-values of the homozygotes after a great number of random-matings. The derivation will be omitted; it is done by means of the same method as used in § 4.

We find that

$$m_\infty : o_\infty : s_\infty : u_\infty : u'_\infty : s'_\infty : o'_\infty : m'_\infty =$$

$$(\varphi . \varphi_{24} . \varphi_{34})^2 : (\varphi . \varphi_{13}\varphi_{34})^2 : (\varphi . \varphi_{12}\varphi_{24})^2 : (\varphi . \varphi_{12}\varphi_{13})^2 : (\varphi_{1234}\varphi_{24}\varphi_{34})^2 :$$
$$(\varphi_{1234}\varphi_{13}\varphi_{34})^2 : (\varphi_{1234}\varphi_{12}\varphi_{24})^2 : (\varphi_{1234}\varphi_{12}\varphi_{13})^2 ; \quad . \; . \; . \; (V)$$

Again the product $m_\infty m'_\infty = o_\infty o'_\infty = s_\infty s'_\infty = u_\infty u'_\infty$, or, in words: the quotient of the numbers of two homozygotes is again constant after a great number of random-matings.

If in the parental population $\left.\begin{aligned} M &= M' \\ O &= O' \\ S &= S' \\ V &= V' \end{aligned}\right\}$ all homozygotes

will be equal in number after a great number of matings according to form (V).

If in a population the homozygotes are proportional to each other in pairs, then the population will be invariable in its constitution, or:

$$\frac{M\Psi^3 + \gamma\Psi^2\{(M+V')\varphi + (M+O)\varphi_{24} + (M+S)\varphi_{34}\} + \delta\Psi.\varphi.\varphi_{24}\varphi_{34}\}}{O\Psi^3 + \gamma\Psi^2\{(O+S')\varphi + (O+V)\varphi_{13} + (O+M)\varphi_{34}\} + \delta\Psi.\varphi.\varphi_{13}\varphi_{34}\}}$$

must be $= \dfrac{M}{O} = \dfrac{S}{V} =$ etc. or,

$$\gamma\Psi\varphi OV' + \gamma\varphi\varphi_{34}OS + \gamma\Psi\varphi_{24}MO + \gamma\Psi\varphi_{24}O^2 + \delta\varphi\varphi_{24}\varphi_{34}O$$

must b =

$$\gamma\Psi\varphi MS' + \gamma\Psi\varphi_{34}MV + \gamma\Psi\varphi_{13}MO + \gamma\Psi\varphi_{13}M^2 + \delta\varphi\varphi_{13}\varphi_{34}M.$$

It is clear that $\gamma\Psi\varphi OV' = \gamma\Psi\varphi MS'$, OV′ and MS′ being equal.

So is $\gamma\Psi\varphi_{34}OS = \gamma\Psi\varphi_{34}MV$, OS and MV being equal.

The following connection must exist:

$$\mathrm{O}\varphi_{24}\{\gamma\Psi(\mathrm{M}+\mathrm{O})+\partial\varphi\varphi_{34}\}=\varphi_{18}\{\mathrm{M}\gamma\Psi(\mathrm{M}+\mathrm{O})+\partial\varphi\varphi_{34}\},\text{ or}$$

$$\mathrm{O}\varphi_{24}\text{ must be }=\mathrm{M}\varphi_{18},\text{ or}$$

$$\mathrm{MM'}+\mathrm{MO}+\mathrm{MS'}+\mathrm{MV}=\mathrm{MO}+\mathrm{OO'}+\mathrm{OS}+\mathrm{OV'}.$$

$\mathrm{MM'}+\mathrm{MS'}=\mathrm{OO'}+\mathrm{OV'}$. To prove this we consider that the homozygotes are proportional in pairs, so

$$\frac{\mathrm{M}}{\mathrm{O}}=\frac{\mathrm{O'}}{\mathrm{M''}},\text{ or }\mathrm{MM'}=\mathrm{OO'}.\ \frac{\mathrm{M}}{\mathrm{O}}=\frac{\mathrm{V'}}{\mathrm{S'}},\text{ or }\mathrm{MS'}=\mathrm{OV'}.$$

Both sides of the equation are identical and our result is that; starting from a population in which the homozygotes are proportional to each other in pairs, we will find that this population is invariable in its constitution, if all matings are equally probable.

The same result we obtained for a population with two mendelian factors (§ 5).

If a population with one factor we had three different groups of organisms, two factors increase the different groups to 3^2.

A population with 4 mendelian factors has already 81 different types. It is clear that the derivation of this formula cannot be that followed in § 3.

In population with more than two factors the derivation of the gamete constitution is a problem by itself.

We will try to find that constitution.

a) If there is one factor, then the gamete A will be formed in the number $\mathrm{A}=2(\mathrm{AA}+\frac{1}{2}\mathrm{Aa})$, if AA; Aa and aa express quantitatively and qualitatively the different groups of individuals.

b) Two factors. The gamete AB is formed in the number $\mathrm{AB}=2\{\mathrm{AABB}+\frac{1}{2}\mathrm{AaBB}+\frac{1}{2}\mathrm{AaBb}+\frac{1}{4}\mathrm{AaBb}\}$.

c) Three factors. The gamete ABC is formed in the number:

$$2\{\mathrm{AABBCC}+\tfrac{1}{2}\mathrm{AaBBCC}+\tfrac{1}{2}\mathrm{AaBBCC}+\tfrac{1}{2}\mathrm{AABBCc}+$$
$$\tfrac{1}{4}\mathrm{AaBbCC}+\tfrac{1}{4}\mathrm{AaBBCc}+\tfrac{1}{4}\mathrm{AABbCc}+\tfrac{1}{8}\mathrm{AaBbCc}\}.$$

It is directly to be seen that, while the homozygote has the coefficient 1, the monoheterozygote $\frac{1}{2}$, the diheterozygote $\frac{1}{2^2}$, the n-heterozygote must have the coefficient $\frac{1}{2^n}$. Further that the number of possible homozygotes, mono-di-tri-etc. heterozygotes are formed according to the coefficients of the binomium $2(p + \frac{1}{2}q)^n$; n being the number of the mendelian factors in the population.

For, working out this binomium we find:

$$2(p+\tfrac{1}{2}q)^n = 2\left[p^n + \frac{n}{1}p^{n-1}\left(\frac{1}{2}\right)q + \frac{n(n-1)}{1\,.\,2}p^{n-2}\left(\frac{1}{2^2}\right)q^2 + \right.$$
$$\left. + \,.\,.\,.\,.\,.\,.\,.\,.\,.\, + \frac{1}{2^n}q^n\right].$$

We found for the constitution of the gamete ABC for instance

$$ABC = 2\{AABBCC + \underbrace{\tfrac{1}{2}AaBBCC + \tfrac{1}{2}AABbCC + \tfrac{1}{2}AABBCc}_{} +$$
$$\underbrace{\tfrac{1}{4}AaBbCC + \tfrac{1}{4}AaBBCc + \tfrac{1}{4}AABbCc}_{} + \tfrac{1}{8}AaBbCc$$

$\frac{n}{1}$ terms with coeff $\frac{1}{2}$; $\frac{n(n-1)}{1\,.\,2}$ terms with coeff $\frac{1}{2^2}$.

If we put the problem in a more general way, and call
G_n the number of the gamete with n mendelian factors;
H „ „ „ „ corresponding homozygote;
N „ „ „ „ „ n heterozygote;
$\Sigma(Y\ I)$ the sum of the corresponding Y monoheterozygotes;
$\Sigma(Z\ II)$ „ „ „ „ „ Z diheterozygotes etc.;
the quantity of the gamete will be in that case:

$$G_n = 2\left[H + \tfrac{1}{2}\Sigma\left\}\frac{n}{1}\,I\right\{ + \frac{1}{2^2}\left\}\frac{n(n-1)}{1\,.\,2}\,II\right\{ + \right.$$
$$\left. \frac{1}{2^3}\left\}\frac{n(n-1)(n-2)}{1\,.\,2\,.\,3}\,III\right\{ + \,.\,.\,.\,.\, + \frac{1}{2^n}N\right]\,.\,.\,(VI).$$

If we ask f. i. for the number of the gamete Ab (§ 3). Form (VI) gives $G_2 = 2\{H + \frac{1}{2}\Sigma(\frac{2}{1}I) + \frac{1}{2^2}N\}$, or

$\mathrm{Ab} = 2\{\mathrm{AAbb} + \tfrac{1}{2}\underbrace{(\mathrm{Aabb} + \mathrm{AABb})}_{\frac{2}{1}} + \tfrac{1}{4}\mathrm{AaBb}\}$, or according to the nomenclature of § 3:

$\mathrm{Ab} = 2o + n + r + \tfrac{1}{2}q$, the same result we obtained before.

§ 9. Starting from a population in which the homozygotes are equal in number, and supposing the same condition for the mono-di- etc. -heterozygotes we will get if G_n and $G_{n'}$ be two gametes

$$G_n = 2[H + \tfrac{1}{2}\sum\left(\frac{n}{1}I\right) + \frac{1}{2^2}\sum\left\{\frac{n(n-1)}{1.2}II\right\} + \ldots\frac{1}{2^n}N].$$

$$G_{n'} = 2[H' + \tfrac{1}{2}\sum\left(\frac{n}{1}I'\right) + \frac{1}{2^2}\sum\left\{\frac{n(n-1)}{1.2}II'\right\} + \ldots\frac{1}{2^n}N']$$

We have $H = H'$, $\sum\left(\frac{n}{1}\,I\right) = \sum\left(\frac{n}{1}\,I'\right)$ (all I's are equal to the I''s) etc. $N = N'$, so we conclude that $G_n = G_{n'}$. In the filial generation the homozygotes will be formed in numbers G_n^2, $G_{n'}^2$ etc. So they are equal in number. The monoheterozygotes in the number $2G_nG_{n'}$, $2G_mG_{m'}$ etc. They are equal in number too. The diheterozygotes in the number $2(G_{nn'} + G_mG_{m'})$ equal to $4G_n^2$ etc. So we see that in the filial generation there exists the following proportion:

homozygote : monoheteroz. : dih.z. : trih.z. : n h.z. =
$1 : 2 : 2^2 : 2^3 : 2^n$ . . . . . . (VII).

For the filial generation we can use the same reasoning. The gametes will be formed again in equal numbers; and the result will be the same.

So the population in which the proportions are expressed by form (VII) is invariable in its constitution.

(A more generalised form of the facts found in § 2 and § 6).

§ 10. More qualities, deduced for two or three characters, can be derived from form (VI)

$$G_n = 2\left[H + \tfrac{1}{2}\sum\left\{\frac{n}{1}\ \mathrm{I}\right\} + \frac{1}{2^2}\left\{\frac{n(n-1)}{1\,.\,2}\ \mathrm{II}\right\} + \ldots\ldots + \frac{1}{2^n}N\right].$$

1) *The homozygote* can be formed only in one way; combination of two similar gametes.

Let us take the most simple case: the gamete is dominant in all its (n) factors. So we can express H qualitatively and quantitatively by G_n^2.

2) *The monoheterozygote* can be formed, according to the formula, in $\frac{n}{1}$ ways.

Always by combination of a „dominant" and a „monorecessive" gamete (f. i. Aa by A and a).

If we call G_{n-1} the monorecessive gamete we will have

$$2\,.\,\tfrac{1}{2}\sum\left\{\frac{n}{1}\ \mathrm{I}\right\} = \sum\frac{n}{1}G_nG_{n-1}$$ monoheterozygotes.

3) *The diheterozygote* can be formed in $\frac{n(n-1)}{1\,.\,2}$ ways, partially by combining G_n with different G_{n-2}'s, and partially by combining G_{n-1} with other G_{n-1}'s. We can write for the total number

$$2\,.\,\frac{1}{2^2}\Sigma G_nG_{n-2} + 2\frac{1}{2^2}\Sigma G_{n-1}G_{n-1};$$ together $\frac{n(n-1)}{1\,.\,2}$ terms.

These considerations will lead to the following formula:

$$G_n^{p+1} = 2[{}^pG_n{}^2 + \sum\frac{n}{1}{}^pG_n{}^pG_{n-1} + \tfrac{1}{2}\Sigma{}^pG_n{}^pG_{n-2} +$$

$$+ \tfrac{1}{2}\Sigma{}^pG_{n-1}{}^pG'_{n-1} + \frac{1}{2^2}\Sigma{}^pG_n{}^p\acute{G}_{n-3} + \frac{1}{2^2}{}^pG_{n-1}{}^pG_{n-2} + \ldots\ldots$$

$$\ldots\ldots + \frac{1}{2^{n-1}}\{{}^pG_n{}^pG_o + \Sigma{}^pG_{n-1}{}^pG_{n-(n-1)} +$$

$$+ \Sigma{}^pG_{n-2}{}^pG_{n-(n-2)} + \ldots\ldots + \Sigma{}^pG_{\frac{1}{2}n}{}^pG'_{\frac{1}{2}n}\}] \quad \ldots\ldots \quad \text{(VIII)}.$$

Remark.

${}^{p+1}G_n$ is the gamete who will form the homozygote ${}^{p+1}G_n^2$ of the $p + 1$ generation; ${}^{p}G_n^2$ is the corresponding homozygote of the p generation. The term $\Sigma {}^{p}G_{\frac{1}{2}n} {}^{p}G_{\frac{1}{2}n}$ is derived supposing n even. If n is odd the term will run $\Sigma {}^{p}G\frac{n+1}{2} {}^{p}G\frac{n-1}{2}$.

4) If in a panmictic population the number of the homozygotes are proportional to each other in pairs (the quotient $\frac{\text{n}^0.\ 1}{\text{n}^0.\ 2}$ being equal to $\frac{\text{n}^0.\ 3}{\text{n}^0.\ 4}$ etc.); we can derive a quality of that population from form (VIII). It is evident that the number of the gametes formed by the homozygotes remain proportional to each other in the same way as the parental individuals were.

In §§ 3 and 7 we wrote the gametes in the following order: ABCDE, aBCDE, AbCDE, abCDE etc.

So $\frac{G_n}{G'_{n-1}} = \frac{G'_{n-1}}{G_{n-2}}$. If we continue that list we will get:

$$= \frac{G''_{n-1}}{G'_{n-2}} = \frac{G''_{n-2}}{G_{n-3}} = \frac{G'''_{n-1}}{G'''_{n-2}} = \frac{G''''_{n-2}}{G'_{n-3}} \text{ etc.; we can conclude}$$

$$G_n G_{n-2} = G_{n-1} G'_{n-1};\ G''_{n-1} G_{n-3} = G''_{n-2} G'_{n-2};$$

$$G'''_{n-1} G'_{n-3} = G'''_{n-2} G''''_{n-2} \text{ etc.}$$

With the help of these facts we can transform ${}^{p+1}G_n$ in the following way:

$${}^{p+1}G_n = 2[{}^{p}G_n^2 + \sum \frac{n}{1} {}^{p}G_n {}^{p}G_{n-1} + \tfrac{1}{2} \sum \frac{n(n-1)}{1.2} {}^{p}G_n {}^{p}G_{n-2} +$$

$$+ \frac{1}{2^2} \sum \frac{n(-1)(n-2)}{1.2.3} {}^{p}G_n {}^{p}G_{n-3} + \ldots + \frac{1}{2^{n-1}} {}^{p}G_n {}^{p}G_o]$$

or,

$${}^{p+1}G_n = 2{}^{p}G_n^2 + 2{}^{p}G_n \Big[\sum \frac{n}{1} {}^{p}G_{n-1} + \tfrac{1}{2} \sum \frac{n(n-1)}{1.2} {}^{p}G_{n-2} +$$

$$+ \frac{1}{2^2} \sum \frac{n(n-1)(n-2)}{1.2.3} {}^{p}G_{n-3} + \ldots + \frac{1}{2^{n-1}} {}^{p}G_o \Big] \ldots \text{(IX)}.$$

We must prove $\frac{{}^{p+1}G_n}{{}^{p+1}G_{n-1}}$ to be constant, let us say

$$\frac{{}^{p+1}G_n}{{}^{p+1}G_{n-1}} = \frac{{}^{p}G_n}{{}^{p}G_{n-1}} \quad \ldots\ldots \quad (c).$$

Now we can write for ${}^{p+1}G_{n-1}$

$$ {}^{p+1}G_{n-1} = 2[{}^{p}G_{n-1}{}^{2} + \sum\frac{n-1}{1}{}^{p}G_{n-1}{}^{p}G_{n-2} +$$

$$+ \tfrac{1}{2}\sum\frac{(n-1)(n-2)}{1\,.\,2}{}^{p}G_{n-1}{}^{p}G_{n-3} +$$

$$+ \frac{1}{2^2}\sum\frac{(n-1)(n-2)(n-3)}{1\,.\,2\,.\,3}{}^{p}G_{n-1}{}^{p}G_{n-4} + \ldots]$$

or,

$$ {}^{p+1}G_{n-1} = 2{}^{p}G_{n-1}{}^{2} + 2{}^{p}G_{n-1}\sum\Big[\frac{n-1}{1}{}^{p}G_{n-2} +$$

$$+ \tfrac{1}{2}\sum\frac{(n-1)(n-2)}{1\,.\,2}{}^{p}G_{n-3} + \ldots\ldots\Big]$$

From condition (c) we can derive that ${}^{p+1}G_n\,.\,{}^{p}G_{n-1}$ must equal ${}^{p+1}G_{n-1}{}^{p}G_n$, and, if we substitute the derived forms for ${}^{p+1}G_n$ and ${}^{p+1}G_{n-1}$ we get

$$ {}^{p+1}G_n{}^{p}G_{n-1}{}^{2} + {}^{p+1}G_n{}^{p}G_{n-1}\sum\frac{n-1}{1}{}^{p}G_{n-2} +$$

$$+ \tfrac{1}{2}{}^{p+1}G_n{}^{p}G_{n-1}\sum\frac{(n-1)(n-2)}{1\,.\,2}{}^{p}G_{n-3} + \ldots \text{ must equal}$$

$$ {}^{p+1}G_{n-1}{}^{p}G_n{}^{2} + {}^{p+1}G_{n-1}{}^{p}G_n\sum\frac{n}{1}{}^{p}G_{n-1} +$$

$$+ \tfrac{1}{2}{}^{p+1}G_{n+1}{}^{p}G_n\sum\frac{n(n-1)}{1\,.\,2}{}^{p}G_{n-2} +$$

$$+ \frac{1}{2^2}{}^{p+1}G_{n-1}{}^{p}G_n\sum\frac{n(n-1)(n-2)}{1\,.\,2\,.\,3}{}^{p}G_{n-3} + \ldots$$

We can devide by ${}^{p+1}G_n{}^{p}G_{n-1}$ and ${}^{p+1}G_{n-1}{}^{p}G_n$, then

$$[{}^{p}G_{n-1} + \sum\frac{n-1}{1}{}^{p}G_{n-2} + \tfrac{1}{2}\sum\frac{(n-1)(n-2)}{1\,.\,2}{}^{p}G_{n-3} + \ldots]$$

must equal

$$\left[{}^{p}G_{n} + \sum \frac{n}{1}{}^{p}G_{n-1} + \frac{1}{2}\sum \frac{n(n-1)}{1\,.\,2}{}^{p}G_{n-2} + \ldots\right] \ldots \ldots \text{(X)}$$

This is the condition for constancy in the population.

§ 11. If we consider again the limitforms of § 4 we can give that form now a more general aspect.

Let M + O equal φ
M + S equal φ_2
O + V equal φ_1
S + V equal φ_{12} we have a nomenclature analogous with the limitforms found for 3 factors (§ 7, form V).

Limitform 2 factors $(\varphi\varphi_2)^2 : (\varphi\varphi_1)^2 : (\varphi_2\varphi_{12})^2 : (\varphi_1\varphi_{12})^2$
3 factors $(\varphi\varphi_{24}\varphi_{34})^2 : (\varphi\varphi_{13}\varphi_{34})^2 : (\varphi\varphi_{12}\varphi_{24})^2 : (\varphi\varphi_{12}\varphi_{13})^2 : (\varphi_{24}\varphi_{34}\varphi_{1234})^2 : (\varphi_{13}\varphi_{34}\varphi_{1234})^2 : (\varphi_{12}\varphi_{24}\varphi_{1234})^2 : (\varphi_{12}\varphi_{13}\varphi_{1234})^2$

we can make the following table.

Value of n.	No. of Factors $\Phi\Phi_1\Phi_2 \ldots$	No. of Sums in a factor $\Phi\Phi_1\Phi_2 \ldots$	No. of factors in a sum Φ.
2	2^2	2	2
3	2^3	3	2^2
4	2^4	4	2^3
5	2^5	5	2^4
⋮	⋮	⋮	⋮
n	2^n	n	2^{n-1}

The limitform of the homozygotes in a panmictic population with n genotypic factors will therefore run as follows:

$$[\overbrace{\underbrace{\varphi(2^{n-1}\text{ terms})\,\varphi_1\varphi_2\ldots}_{n\text{ terms}}]^2 : [\underbrace{\varphi'\varphi'_1\varphi'_2\ldots}_{n\text{ terms}}]^2 ; [\varphi''_1\varphi''_2\ldots]^2 : [\ldots\ldots]^2 :}^{2^n\text{ terms}} \quad \ldots\ldots (XI)$$

We can find per analogiam the values φ etc.

I was not able to *prove* this form for n factors.

Perhaps a mathematician will take interest in these questions and work out the forms whose derivation is above the powers of a biologist.

I only wanted to give a rough theoretical outline for a more general theory of „mathematical mendelism", the panmictic population with n factors being the most general case.

Practical forms will result from such a base with much fester foundation and in much more systematical place as hitherto was the case.

It is clear that Pearsons „Law of ancestral heridity" ought to be revised after the results obtained. The composition of a generalised mendelian population *is not stable.*

So his laws 1e that the regression for any ancestor and the offspring was linear, and 2e that the correlations decreased in a geometrical progression, are derived for the population $S_1(AA) + 2S_3(Aa) + S_2(aa)$ (Pearson 1909).

Biologists attaching much importance to the facts of „regression" and „correlation" will perhaps derive the forms for the more general case.

§ 12. The obtained results are practical applicable for a population mating at random, with known constitution:

1e. To determine the number of matings;

2e. To determine the number of mendelian factors;

3e. To verify the random mating.

They can form a link between experimental mendelism and its application on phenomena in wild populations.

The wild populations are subjects of mendelian laws as well as laboratory cultures. Many biologists seem to forget that.

But the methods with which we work in the free nature must differ from that in the laboratory. They must differ as much as chemistry and geology differ. Applying this reasoning on our subject we could try:

1e. To find an isolated population;

2e. Verify its gametic and genetic constitution;

3e. Apply the corresponding formula on that population.

These and similar forms give us a key for a new field of research, that, just as ecology does, works in the free nature.

Especially endemic populations on small islands (were countings are possible) could be fertile fields for such a research.

Augs.—Dec. 1918.

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APPENDIX.

The analytical treatment of the form found for two factors throws more light upon the relations of the different generations. Therefore I will try to apply that method.

$$m = 2^{(2^n-2n)} \, . \, \Psi^{(2^n-2)} \left\{ M + (2^{n-1} - 1) \frac{(M + O)(M + S)}{\Psi} \right\}^2$$

is the number of the homozygote m.

The whole population has after n generations the number: $2^{2^n} \Psi^{2^n}$, so the fraction

$$\frac{2^{(2^n-2n)} \Psi^{(2^n-2)} \left\{ M + (2^{n-1} - 1) \frac{(M + O)(M + S)}{\Psi} \right\}^2}{2^{2^n} \Psi^{2^n}}$$

expresses the part of the homozygotes in the population.

This is

$$2^{-2n} \Psi^{-2} \left\{ M + (2^{n-1} - 1) \frac{(M + O)(M + S)}{\Psi} \right\}^2.$$

The contribution of the AB gametes in the total number of gametes is the square root of that form.

This will be

$$2^{-n} \frac{M}{\Psi} - 2^{-n} \frac{(M + O)(M + S)}{\Psi^2} + \frac{(M + O)(M + S)}{2\Psi^2}.$$

We can prove that the whole form never will be greater than $\frac{1}{2}$, which is omitted here.

The gamete fraction $y = f(x)$, x being the number of generations that panmictic mating has taken place.

$$y = 2^{-n} \left\{ \frac{M}{\Psi} - \frac{(M + O)(M + S)}{\Psi^2} \right\} + \frac{(M + O)(M + S)}{2\Psi^2}.$$

We can write that: $y = 2^{-x}A + B$, an exponential function (see figure).

This function is assymptotic for $x = \infty$, to a straight line $y = B$, the same result we obtained before in the mathematical treatment.

The function is discontinuous. This is caused by the fact that x is always a whole number.

We can treat it as if it was a continuous function.

Here follows the list for the expression $y = f(x)$.

$x = \infty;\ y = B$ $\quad$ $x = -\infty;\ y = \infty$
$x = 4\ ;\ y = \frac{1}{16}A + B$ $\quad$ $x = -4\ ;\ y = 16A + B$
$x = 3\ ;\ y = \frac{1}{8}A + B$ $\quad$ $x = -3\ ;\ y = 8A + B$
$x = 2\ ;\ y = \frac{1}{4}A + B$ $\quad$ $x = -2\ ;\ y = 4A + B$
$x = 1\ ;\ y = \frac{1}{2}A + B$ $\quad$ $x = -1\ ;\ y = 2A + B$
$x = 0\ ;\ y = A + B$ $\quad$ $x = 0\ ;\ y = A + B.$

The negative values of x express the case that the panmixy took already place before the F_1 generation. The values are impossible if the corresponding $y > \frac{1}{2}$ or $y < 0$.

The first assumption should lead to the fact that the part of m in the population was greater than the whole population; the second to the fact that there existed negative numbers of gametes. We can draw a line $y = \frac{1}{2}$ (line V) above which line no real values for y are possible.

2) The form of the curve is in a high degree dependent of the coefficients A and B, especially of M (the formula expresses the number of the M gamete; we can adapt it by cyclic substitution for other gametes).

1st Case.

$M = \infty$

$$y = 2^{-x}\left\{\frac{M}{\Psi} - \frac{(M+O)(M+S)}{\Psi^2} + \frac{(M+O)(M+S)}{2\Psi^2}\right.$$

$\Psi^2 y = 2^{-x}\{M\Psi - (M+O)(M+S)\} + \frac{1}{2}(M+O)(M+S)$, or,

$$(M^2 + O^2 + S^2 + V^2 + 2MO + 2MS + 2MV + 2SO + 2OV + 2SV)y =$$

$$2^{-x}(M^2 + MO + MS + MV - M^2 - MO - MS - OS) + \\ + \tfrac{1}{2}(M^2 + MO + MS + OS).$$

Division by M^2 gives, all fractions being = zero:

$y = \frac{1}{2}$ (the population is invariant and consists only of individuals AABB) (line V).

2nd Case.

M = O the form is changed in

$$y = 2^{-x}\left(-\frac{OS}{\Psi^2}\right) + \frac{OS}{2\Psi^2} \text{ or } y = (2^{-1} - 2^{-x})\frac{OS}{\Psi^2} \text{ (line I).}$$

The form of this curve is expressed by the following table:

$x = \infty$; $y = B$ $\qquad$ $x = -\infty$; $y = -\infty$
$x = 4$; $y = \frac{1}{8}B$ $\qquad$ $x = -4$; $y = -31B$
$x = 3$; $y = \frac{3}{4}B$ $\qquad$ $x = -3$; $y = -15B$
$x = 2$; $y = \frac{1}{2}B$ $\qquad$ $x = -2$; $y = -7B$
$x = 1$; $y = 0$ $\qquad$ $x = -1$; $y = -3B$
$x = 0$; $y = -B$ $\qquad$ $x = 0$; $y = -B$.

3d Case.

$M = \frac{OS}{V}$. y is, as we derived before $\frac{(M+O)(M+S)}{2\Psi^2}$, or, MV being = OS $y = \frac{M}{2\Psi}$, being a straight line, the population is invariant (line III).

4th Case.

M = O = S = V, all gametes were formed in equal number in the F_1

$$y = 2^{-x}\left\{\frac{M}{4M} - \frac{4M^2}{16M^2}\right\} + \frac{4M^2}{32M^2} \quad y = \tfrac{1}{8} \text{ (line II).}$$

The figure expresses the area of the curvebundle $y = 2^{-x}A + B$ for different values of M.

The vertically lined area is the possible area, the horizontal lined piece is possible if panmixy took place before the F_1 generation. The dotted lines are values never reached in reality.

3) A measure for the changement in the number of homozygotes in following generations is the differential quotient

$$y = 2^{-x}A + B$$

$$\frac{dy}{dx} = 2^{-x}A \ln 2.$$

For $x = o$ we get the changement parallel to $A \ln 2$. We call A the *„modulus of changement"*.

What is the signification of A and how does its value change?

We can write $A = \frac{MV - OS}{\Psi^2}$, this value has a maximum for $OS = O$, the coefficient is in that case $\frac{MV}{M+V}$.

The graph shows us that either A or B will be maximal if $A + B = \frac{1}{2}$.

In that case

$$\frac{M}{\Psi} - \frac{(M+O)(M+S)}{\Psi^2} + \frac{(M+O)(M+S)}{2\Psi^2} = \tfrac{1}{2} \text{ or}$$

$$\frac{M}{\Psi} - \frac{(M+O)(M+S)}{2\Psi^2} = \tfrac{1}{2}$$

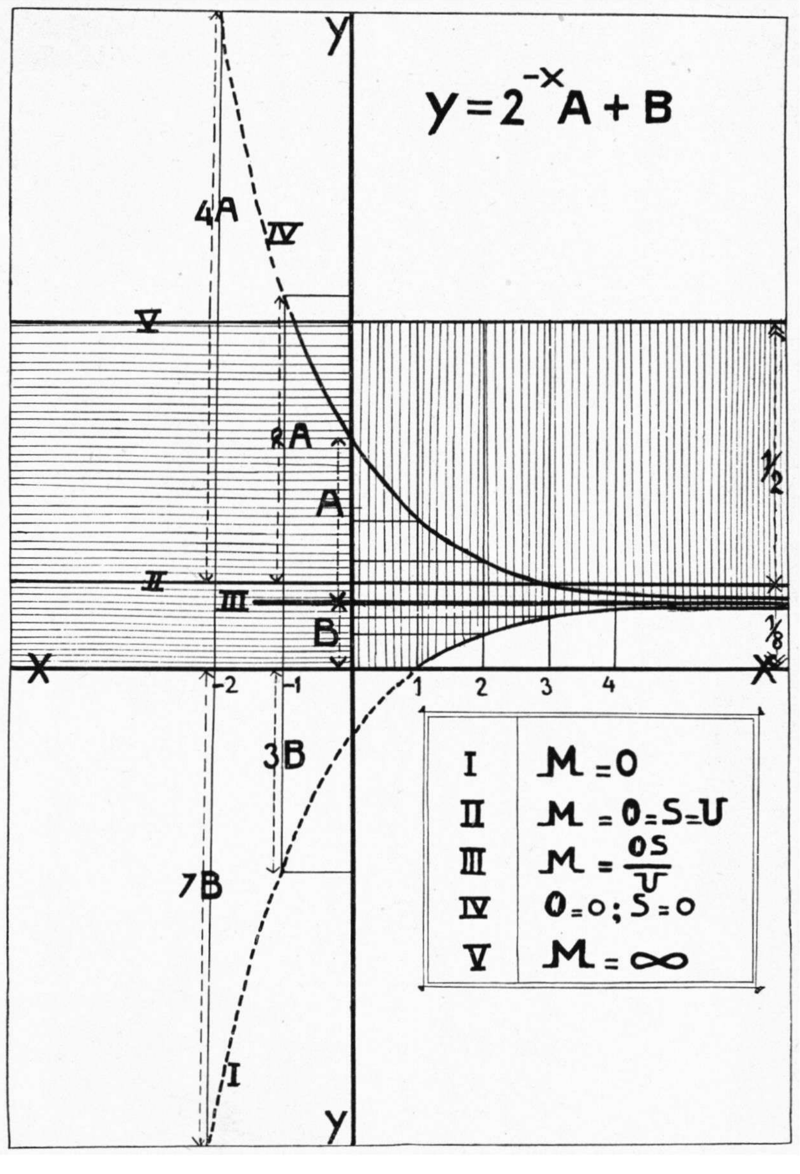
$$2M^2 + 2MO + 2MS + 2MV - M^2 - MO - MS - OS =$$
$$M^2+S^2+O^2+V^2+2MO+2MS+2MV+2OS+2OV+2SV$$
$$S^2 + O^2 + V^2 + 3OS + MS + MO + 2OV + 2SV = o.$$

This condition is fulfilled if $\begin{cases} S = o \\ O = o \\ V = o. \end{cases}$

In that case A will be $\frac{M}{M} - \frac{M^2}{M^2} = o$. $B = \frac{1}{2}$, the same result we obtained by putting $M = \infty$.

By putting $A = \frac{1}{2}$ we get $\frac{VM - OS}{\Psi^2} = \frac{1}{2}$ Calculation gives us the condition that $M \pm S = O = V =$ zero.

In the case of $A = \frac{1}{2}$ the population does not exist!


Y
y = 2^-x A + B
4A
IV
V
2A
A
II
III
B
X
-2
-1
1
2
3
4
1/2
1/8
X
3B
7B
I
Y
I M = 0
II M = O = S = U
III M = OS/U
IV O = o ; S = o
V M = ∞

So we have shown that A varies from zero to $\frac{MV}{M+V}$.

The results of experimental researches can be tested by means of the graph. We can find A and B

$$y = 2^{-x}\left\{\frac{M}{\Psi} - \frac{(M+O)(M+S)}{\Psi^2}\right\} + \frac{(M+O)(M+S)}{2\Psi^2} \text{ or}$$

$A + 2B = \frac{M}{\Psi}$. $\frac{M^2}{\Psi^2}$ is the part of the homozygote M in the original population.

The graph gives a simple test for panmixy in an exponential curve:

We sum up A and 2B, draw a line in the same scale, in length equal to the parental population and state graphically on millimeterpaper their relation.

We can apply the same method on a population with three factors.