that “eumelanin and pheomelanin can sometimes be confused phenotypically” may well be extended to birds.

The only indigo (In)-carrying specimen (no. 15) in our material was an “Andalussian,” a blue black or gun metal coloration that is caused by the combination of S and heterozygous In on a wild-type background (Levi 1963; Sell 1986). When compared with the same genetic background lacking In (no. 9), the eumelanin concentration of the vanes is reduced in the “Andalussian” to one-half to one-third, which corresponds with the visual impression of the plumage (black vs. blue black). In this genetic constellation pheomelanin levels seem not to be affected by In.

In pigeons with the wild-type color locus and S factor, the mutants In (no. 15) and d (no. 12) result in almost identical eumelanin and pheomelanin concentrations. Nevertheless, birds with these genetic combinations are clearly separable by their visual appearance (blue black vs. dun). This could be due to the fact that our method for quantification of eumelanin does not distinguish brown from black eumelanin. From the optical impression it would seem that the depressing effect of d on eumelanin contents mainly affects the black form of the pigment.

From the Institut für Haustierkunde, Christian-Albrechts-Universität, 2300 Kiel 1, Germany (Haase); the School of Hygiene, Fujita Health University, Toyoake, Aichi 470-11, Japan (Ito and Wakamatsu), and the Institut für Weltwirtschaft und Internationales Management der Universität, 2800 Bremen 33, Germany (Sell).

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References

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breeding coefficient designated $F_T$ were done as follows.

Methods and Results

Calculations of the inbreeding coefficient done as follows.

Tuberosum × diploid species. The tetraploid Tuberosum (T) parent has an inbreeding coefficient designated $F_T$. The diploid species parent (Z) has an inbreeding coefficient designated $F_Z$. Thus, the inbreeding coefficient of the derived tetraploid (DT) is

$$F_{DT} = (1/6)[P(x_1 = x_2) + P(x_1 = x_3) + P(x_1 = x_4) + P(x_2 = x_3) + P(x_2 = x_4) + P(x_3 = x_4)].$$

which is

$$F_{DT} = (1/6)[F_T + 40_{TZ} + F_Z].$$

where $x_1$ and $x_2$ are alleles inherited from the tetraploid Tuberosum parent, assuming chromosomal segregation, and $x_3$ and $x_4$ are alleles inherited from the diploid species parent.

If the coefficient of double reduction ($\alpha$) is greater than zero, the $P(x_1 = x_2) = \alpha + (1 - \alpha)F_T$, as shown by Kempthorne (1957). Now, the probability that $x_1 = x_2$ will be a function of the inbreeding coefficient of the diploid, the mechanism of $2n$ pollen production, and the frequency of single exchange tetrads. In the diploid species parent, $P(x_1 = x_2) = F_2$ and, therefore, it follows that $P(x_1 = x_2) = 1 - F_2$. Thus, the probability that the diploid species parent will be capable of producing three types of $2n$ gametes (i.e., $x_1x_2$, $x_1x_3$, and $x_1x_4$) is equal to $1 - F_2$. In the case of first-division restitution, these $2n$ gametes are produced with frequencies of $\beta/4$, $1 - \beta/2$, and $\beta/4$, respectively. The rest of the $2n$ gametes produced by a diploid species parent with an inbreeding coefficient $F_Z$ will be $x_3x_4$ with a frequency of $F_2$.

Therefore, the probability that $x_1 = x_3$ is equal to $F_2 + (1 - F_2)(\beta/4 + \beta/4)$, which equals $\beta/2 + (1 - \beta/2)F_2$. In the FDR case the inbreeding coefficient of the DT will be

$$F_{DT} = (1/6)[\alpha + (1 - \alpha)F_T + 40_{TZ} + (1 - \beta + \beta F_T)].$$

As we have seen earlier, $P(x_1 = x_2) = \alpha + (1 - \alpha)F_{T_2}$. If the T1 and T2 Tuberosum parents are related, $P(x_1 = x_2) = P(x_1 = x_3) = \theta_{TT_2}$; otherwise $P(x_1 = x_2) = P(x_1 = x_3) = 0$. Assuming that the diploid species parent and the Tuberosum parents are unrelated, $P(x_1 = x_2) = P(x_1 = x_3) = 0$, and, if $2n$ pollen is produced by an FDR mechanism, $P(x_1 = x_2) = \beta/2$. If $2n$ pollen is produced by an SDR mechanism, $P(x_1 = x_2) = (1 - \beta)$. By gathering appropriate terms together we see that if the T1 and T2 parents are related to each other but not to the diploid species parents,

$$F_{DT} = (1/6)[\alpha + (1 - \alpha)F_T + 40_{TZ} + (1 - \beta + \beta F_T)].$$

for the case where $2n$ pollen is produced by an SDR mechanism. If $2n$ pollen is produced by an SDR mechanism, then

$$F_{DT} = (1/6)[\alpha + (1 - \alpha)F_T + 20_{TZ} + \beta F_T].$$

If T1 and T2 are related to each other or to the diploid species parent and if $2n$ pollen is produced by an SDR mechanism, then

$$F_{DT} = (1/6)[\alpha + (1 - \alpha)F_T + (1 - \beta + \beta F_T)].$$

If T1 and T2 are related to each other or to the diploid species parent and if $2n$ pollen is produced by an SDR mechanism, then
If the diploid species are unrelated, metes by an SDR mechanism, then this simplifies to
\[ F_{OT} = (1/6)[\alpha + (1 - \alpha)F_{T^2} + 1 - \beta]. \]

If the diploid species parent and the Tube-
rosom species are related, then 
\[ F(x_2 = x_2) = \theta_{T_2z_2} \text{ and } P(x_2 = x_2 = \theta_{T_1z_1} + (1 - \theta_{T_1z_1})/2 \text{ if } 2n \text{ pollen is produced by an FDR mechanism.} \]

By gathering appropriate terms together we see that if the T1 and T2 parents are related to each other and to the diploid species parent, then
\[ F_{OT} = (1/6)[\alpha + (1 - \alpha)F_{T^2} + 2\theta_{T_1z_1} + 2\theta_{T_2z_2} + \theta_{T_1z_1} + (1 - \theta_{T_1z_1})(1 - \beta)]. \]

for the case where 2n pollen is produced by an FDR mechanism. If 2n pollen is produced by an SDR mechanism, then
\[ F_{OT} = (1/6)[\alpha + (1 - \alpha)F_{T^2} + 2\theta_{T_1z_1} + 2\theta_{T_2z_2} + \theta_{T_1z_1} + (1 - \theta_{T_1z_1})(1 - \beta)]. \]

### Discussion

The inbreeding coefficients of derived tetra-
ploids for the three breeding methods using diploid 2n gamete-producing species are summarized in Table 1.

The inbreeding coefficients of tetraploids derived from 4x-2x or 2x-2x hybridizations are complex functions of the coancestry of the parents, the inbreeding of the parents, and the frequency of single exchange tetrads in the diploid parent(s), and they depend on the mechanism of 2n pollen formation. The inbreeding coefficient of derived tetraploids from 4x-2x hybridizations has an additional component comprised of the coefficient of double reduction in the tetraploid parent.

Where the diploid species in Tuberos-
sum × haploid-species hybridizations is unrelated to either tetraploid parent, inbreeding in the derived tetraploid will occur due to inbreeding in the tetraploid Tuberosum parent, the coancestry between the Tuberosum parent and the hap-
loid-species parent, the coefficient of double reduction in the tetraploid Tuberosum parent, and the frequency of single exchange tetrads in the haploid-species hy-
brid. These inbreeding coefficients are the most complex of the three breeding strategies considered, and they have the po-
tential to be the largest.

Where the diploid species in 2x-2x hy-
bridizations are unrelated to each other and are non-inbred themselves, consider-
able inbreeding is still possible in the derived tetraploid. In this case, if 2n pollen and 2n ovules are produced by an FDR mechanism, then 0 ≤ F_{OT} ≤ 1/6. If 2n pol-
len and 2n ovules are produced by an SDR mechanism, then 0 ≤ F_{OT} ≤ 1/3. If the uniting 2n pollen and 2n ovule are produced by different mechanisms, then 0 ≤ F_{OT} ≤ 1/4.
this paper emphasize the importance of considering the genetic relationships in any breeding program that involves interspecific and interploidy hybridizations.

From the U.S. Department of Agriculture, Agricultural Research Service, Vegetable Laboratory, Plant Sciences Institute, Beltsville, MD 20705. Thanks to Dr. George C. C. Tai of Agriculture Canada for his critical reading of the manuscript and helpful suggestions. Ad- dress reprint requests to the author at the address above.

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References
Mok DWS and Peloquin SJ, 1975a. Breeding value of


Genetics of Five Cytoplasmically Inherited Yellow Foliar Mutants in Soybean
S. R. Cianzio and R. G. Palmer

Both nuclear- and cytoplasmic-chlorophyll-deficient mutants are known in soybean [Glycine max (L.) Merr.]. Five chlorophyll-deficient mutants were identified in our research program. Our objectives were to conduct inheritance studies of these mutants, to perform allelism tests of unknown mutants with known mutants, and to determine if nuclear-cytoplasmic interactions occurred. Genetic tests with all five mutants indicated that the yellow foliage phenotype was inherited unaparently in each case through the maternal parent. These five cytoplasmically inherited mutants were added to the Soybean Genetic Type Collection and assigned gene symbols and T numbers. T314 was assigned to gene symbol cyt-Ya. T315 was assigned to cyt-Yb, T316 was assigned to cyt-Yc, T318 was assigned to cyt-Yd, and T320 was assigned to cyt-Ye.

Chlorophyll-deficient mutants are useful as marker genes in genetic studies, as well as in physiology and biochemical research. Some of these mutants are of nuclear origin, whereas others are of cytoplasmic origin. In soybean [Glycine max (L.) Merr.], 36 single-gene recessive nuclear mutants and three cytoplasmic mutants, with various levels of chlorophyll deficiency, are known collectively as chlorophyll-deficient types. These mutants are in the Soybean Genetic Type Collection at the University of Illinois, Urbana, and are identified by T numbers.

The soybean chloroplast genome is inherited maternally (Hatfield et al. 1985).

Restriction fragment length polymorphisms have been used to detect intragenic sequence diversity in the genus Glycine subgenus soja chloroplast DNA (Close et al. 1989; Shoemaker et al. 1986). The mutant genotype cyt-Yb (T278M) produces plants of two types—some that are chlorophyll chimeras, and others that are very weak yellow plants—traits that are inherited cytoplasmically (Shoemaker et al. 1985). In addition to T278M, the other two cytoplasmically inherited soybean mutants are T104 (cyt-G, green seed embryo) and T275 (cyt-Y6, yellow foliage) (Palmer and Kilien 1987).

Both T275 and T278M were identified among progeny of chimeric plants and have been characterized genetically, biochemically, and microscopically. Leaves from cyt-Y6 plants grown in the growth chamber accumulated 77% of the chlorophyll accumulated by green plants also grown in a growth chamber. Leaves from field-grown cyt-Y6 plants accumulated only 38% of the chlorophyll accumulated by field-grown green plants. Electron photomicrographs showed that the plasmid body and chloroplast ultrastructure were normal in cyt-Y6 plants (Palmer and Mascia 1980).

Mutant T278M (cyt-Yb) is maintained in the chimeric form because cyt-Y6 plants are very weak and usually are lethal when grown in the field. Shoemaker et al. (1985) reported that plastid ultrastructure of cyt-Y6 plants seemed normal at 90 microin- steins M-2. At 600 and 2060 microin- steins, cyt-Y6 plastids lacked a structural thylakoid, total chlorophyll content measured at 600 microinsteins was only 28%, and at 2060 microinsteins it was only 1% of green plants.

Interactions of nuclear genomes with orogenelle genomes can take the form of metabolite and energy exchange (Diethelm et al. 1989), co-production of enzyme subunits (Dayé et al. 1989), and co-production of the membrane structural and organizational components (Wallace 1982). A possible nuclear-cytoplasmic interaction was evident in crosses between T275 and T253 (y20-k2) (Palmer and Cianzio 1985). T275 is a chlorophyll-deficient mutant inherited cytoplasmically and identified as cyt-Y6 (Palmer and Mascia 1980). T253 is a chlorophyll-deficient mutant with tan-saddle-pattern seeds (Palmer 1984). Both traits are nuclearly inherited and identified as y20-k2, and they cannot be separated by classical genetic tests into two separate components, y20 and k2 (Palmer 1984). Palmer and Cianzio (1985)