Yield Efficiency of the X-Ray Mutant Svalöf's 'Pallas barley' *

(A biometrical analysis of some Danish data)

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Summary. Svalöf's Pallas barley is an X-ray mutant of the high-yielding Bonus barley variety. Both varieties were released by the Swedish Seed Association, Svalöf, and have gained wide distribution. Pallas barley arose as an erectoides mutant in 1947. After careful testing it was approved in 1958 as an original Swedish variety. It soon became widespread over great parts of western Europe owing to its high productivity, pronounced lodging resistance and high nitrogen utilization.

Danish tests of barley varieties are recorded and published yearly. From 1958 when Pallas entered the Danish trials, and up to and including 1964, its parent Bonus barley was the official Danish standard variety. In 1965 it was replaced by Pallas barley. A careful biometrical comparison of the two varieties has been made with regard to grain yield, lodging resistance, straw height and strawproduction. In addition, the influence of increased lodging resistance on yield as well as the variance of yield and lodging have been analysed.

Background

Erectoides-32 is an X-ray mutant from Svalöf's Bonus barley (Gustafsson, 1954), isolated 1947 in the X_2 generation and later on referred to the gene locus ert-*k* (Hagberg, 1954). From 1951/52 and onwards it was included in yield trials (Fröier, 1954), first under the provisional name of "Svalöf 04032". In 1958 it was officially approved as an "original variety" and given the name "Svalöf's original Pallas barley" (Borg et al., 1958; Borg, 1959; Gustafsson, 1963). It soon became widespread in South Sweden, Denmark, England, Scotland and Ireland. Under certain conditions it has yielded extremely well. In fact, it was advertised in Great Britain 1962 under the slogan: „The three ton barley. All records broken".

Bonus barley, from which erectoides-32 (ert-k^{32}) arose, was a result of Nilsson-Ehle's breeding work at Svalöf (Maja × Seger × Opal, Fröier, 1954). Consequently, both varieties, parent and mutant, were isolated in Svalöf soils. The mutant was detected by its typical erectoides ear, although the erectoid character was not specially extreme. From the beginning it was found to be high-yielding and in addition superior to its parent variety in lodging resistance (analysed in the articles quoted above). In other characteristics, practically important, for instance straw breakage at maturity and susceptibility to mildew, it reacts like its parent. In early Swedish experiments its yielding ability was shown to be similar, if not identical to that of Bonus. As numerous other erectoid mutants Pallas barley has a property most important in modern agriculture: its "nitrogen preference". The mutant prospers, relatively seen, under increasing nitrogen dressings and in fertile soils. It was denoted a "nitrogen ecotype" by Gustafsson (1954, pp. 620–622). Hagberg, in a paper of 1963, classified Pallas "as the best variety in South Sweden" and emphasized its high yielding ability and lodging resistance, also its high protein quality and its resistance to loose smut.

* This paper is cordially dedicated to Professor Hans Stubbe in appreciation of his pioneer research on induced mutations in cultivated plants.

Pallas barley in Danish trials

In 1958, under the name of Sv. 04032, Pallas barley entered the Danish yield trials. Fortunately, from 1957 to 1964, its parent Bonus was used as standard variety in Danish barley trials. In 1965 Pallas replaced Bonus as the official standard. According to information published by Thögersen (1965 b) Pallas had up to and including 1964 been tested in 363 comparative Danish yield trials and on an average yielded 2 per cent more grain than Bonus. It was definitely less lodging. Twenty-one varieties were included in his list of tested varieties (l. c., pp. 108–109). The variety order with regard to grain yields, using Bonus as standard (= 100), was up to 1964 the following:

Pallas = Deba	102%
Swallow = Amsel	101%
Vada = Bonus	100%
Carlsberg II = Proctor = Dana = Minerva = Impala	99%
Sejet 1732 = Hafnia = Ingrid	98%
Herta	97%
Mentor = Maja = Drost A = Freja	96%
Rika	95%
Mari	92%.

It is interesting to note that Pallas was superior to 19 of the 20 other varieties listed, inferior to none of them. Moreover it was by 4 to 7 per cent superior to the well-known Swedish varieties Weibull's Ingrid, Herta and Rika, which had then been compared to Bonus in 510, 248 and 353 trials respectively. The English variety Proctor, tested together with Bonus in 608 trials, yielded 1 per cent less than the standard and 3 per cent less than Pallas. Svalöf's Foma barley (p. 89), in 1964 compared to Bonus in 70 trials, was inferior to this variety by 4 per cent and consequently to Pallas by some 6 per cent.

Yield efficiency of Pallas and Bonus barley in Zealand

The Danish island of Zealand (Fig. 1) is characterized by a type of climate and soil, rather similar to the most fertile region of South Sweden (in the province of Scania). Thögersen (1959–1965) has yearly since 1958, when Pallas entered the Danish trials, reported about its Zealand behaviour. These data are continually being printed and quickly made available to interested farmers, breeders and geneticists. Owing to these circumstances we have considered it appropriate to select just the Zealand data for a detailed biometrical study.

The yield evaluation of the two varieties covers a period of eight years (1958–1965). In all years the grain yields were determined, chiefly in varying localities of the island. Each trial is built on replications. In his publications THÖGERSEN presents individual trial means and these are considered here. Additional information is available for important characteristics like lodging, straw height, straw production, to some extent also for mildew and nematode resistance, grain weights (1000 kernel weight, hectolitre weight) etc. For our analysis the grain yields, absolutely and relatively, alone and in connection with the lodging properties, have been in the foreground.

The following computations were carried out:

1—3: A one-sided analysis of variance with regard to yield ability.
  (1) The variable was the difference in yield of Pallas and Bonus in the respective year and locality.
  (2) The variable was the quotient in yield of the two varieties.
  (3) In this case the variable was the quotient of the Pallas-Bonus differences related to the yield level of the corresponding year. The yield level was measured as the mean value of Pallas-Bonus yields over all localities within years.

4: A one-sided analysis of variance with regard to the lodging properties of Pallas and Bonus.

5—7: A regression-variance analysis of the connection between yield and lodging.
  (5) As (1) above — differences are considered.
  (6) As (2) — quotients.
  (7) As (3) — quotients in relation to the yearly yield level.

8: A one-sided analysis of the variance of straw height.

9: An analysis of the components of variance (within years, between localities, between years) considering yield performance and lodging resistance.

10: Some data on straw yield and total yield (grain plus straw) are discussed.

(1) There are 117 values of differences in yield between Pallas and Bonus. The mean values, for all years and all localities, amount to 49.55 and 48.57 decitons of grain per hectare for Pallas and Bonus respectively (one deciton equal to 100 kilograms), giving a difference between the varieties of 98 kilograms/hectare, or 2 per cent.

The *t*-test has been applied in the statistical analysis: $t = \sqrt{N} \cdot (\bar{x} - m)/s$, where N denotes degrees of freedom (number of observations minus number of years), $\bar{x}$ is the total mean difference, m is a hypothetical value and s is the standard deviation. Applying the value $m = 0$ in this function, we can test whether there exists a significant yield difference between the varieties or not.

We find that

$$\bar{x} = 0.984\,, \quad s = 3.15\,, \quad t = 3.20^{**}.$$

There is no indication of any variation in yield differences between localities and years. The varietal difference is significant on the 1 per cent level.

(2) In this analysis the yield quotient of the varieties is tested against the value 1.0. We find that

$$\bar{x} = 1.0215\,, \quad s = 0.0663\,, \quad r = 3.38^{***}.$$

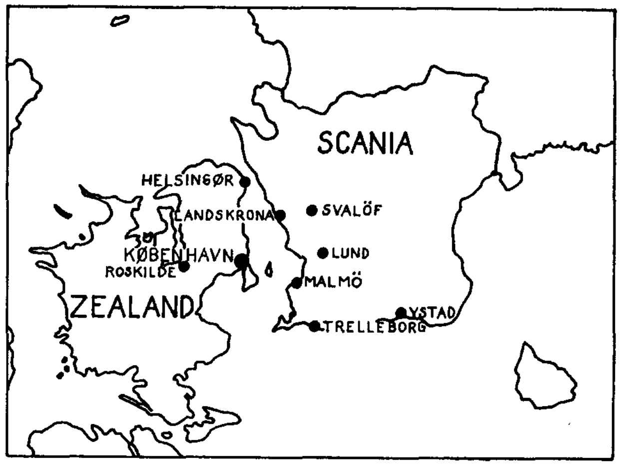

Fig. 1. The Danish island of Zealand.

No differences between localities and years. A highly significant difference in yield (on the 0.1% level).

(3) In this case the varying yield levels of the years are taken into account. As in (1) the quotients of yield performance are tested against a value 0.

$$\bar{x} = 0.0198\,, \quad s = 0.0632\,, \quad t = 3.27^{**}\,.$$

No significant differences between localities or years. The varietal difference is on the 1 per cent level.

According to analysis (1) Pallas is superior to Bonus by 2.03 per cent, according to (2) and (3) by 2.15 and 1.98 per cent. In consequence, independently of the computation method, Pallas significantly differs from Bonus by almost exactly 2 per cent.

(4) The average lodging, in all localities and years, is for Pallas 4.506, for Bonus 6.092 (10 denotes complete lodging, 1 complete erectness). The negative difference (−1.586) indicates that Pallas is less susceptible to lodging than Bonus.

$$x = -1.59\,, \quad s = 1.23\,, \quad t = 13.61^{***}\,.$$

The difference is highly significant. In addition, there is a significant difference between years (0.084**). Below, under (9), it will be shown that Pallas as well as Bonus show conspicuous annual variations in lodging, but also the difference in lodging of the two varieties varies from year to year. There is no consistent parallel variation in this respect.

With regard to yielding ability (1—3) three different methods of evaluation were used. The preceding analysis of lodging resistance corresponds to method (1). Applying the quotient relationship of (2), we find that

$$\bar{x} = 0.724\,, \quad s = 0.230\,, \quad \text{deviation between years} = 0{,}084^{**}\,, \quad t = 12.54^{***}.$$

Similarly, applying method (3) relating to the yield level of the year, we find that

$$\bar{x} = -0.327\,, \quad s = 0.266\,,$$
$$\text{deviation between years} = 0.130^{***} \quad t = 12.82^{***}\,.$$

Generally, the increase in lodging resistance amounts to circa 30 per cent for Pallas as compared to Bonus ($4_1 = 26\%$, $4_2 = 28\%$, $4_3 = 33\%$).

(5) The results under (4) prove that the lodging resistance is higher in Pallas than in Bonus (a well-known fact) and, in addition, that the difference in lodging between the varieties varies with the annual

conditions. There exists then a possibility that the difference in yielding ability, described under (1—3), is causally connected with the difference in lodging resistance, described under (4_1—4_3). This problem has been analysed by determining the correlation of lodging resistance and yield. Similar methods of calculation as under (1—3) can be applied. It is immediately apparent that the difference in yield of Pallas and Bonus and their corresponding difference in lodging are significantly and negatively correlated (correlation coefficient = — 0.235**).

We find the following function of the connection of the two variables ($\bar{x}$ = yield difference of Pallas and Bonus in decitons/hectare, and z = lodging difference between Pallas and Bonus)

$$x = -0.0430 - 0.6458 \cdot z .$$

If $z = 0$ (i.e. the lodging of the varieties is exactly alike), there is no difference in yielding ability ($t = 0.15°$), nor is there any variation between years.

From a biometrical point of view the interpretation is quite simple: If, by some means, the lodging resistance of Bonus could be raised to the level of Pallas, without any change in specific productivity, the two varieties should yield exactly alike. Pallas is a one-factor mutant out of Bonus. There is no indication of any unlinked background mutations having occurred at the time of the ert-mutation. The erectoid mutation (ert-*k*) has greatly changed the internode structure of the straw and increased the lodging resistance. Owing to less lodging, the relative yield level of Pallas is increasing (at least under the soil and climate conditions of Zealand).

The following regressions (6 and 7) confirm the analysis under (5).

(6) Correlation coefficient = — 0.098

x = quotient between Pallas and Bonus yields.

z = quotient between Pallas and Bonus in lodging resistance.

$$x = 1.0494 - 0.386 \cdot z .$$

If $z = 1$, $x = 1.0108$. No yield difference between Pallas and Bonus, when lodging is identical ($t = 1.69°$), no difference between years.

(7) Correlation coefficient = — 0.158

x = quotient between the yield difference of Pallas and Bonus and the productivity level of the year.

z = the corresponding quotient of lodging resistance.

$$x = 1.0009 - 0.0579 \cdot z.$$

If $z = 0$, $x = 1.0009$. No yield difference between Pallas and Bonus in the case of identical lodging ($t = 0.15°$), no difference between years.

(8) The variable is the difference in straw height between Pallas and Bonus. Measurements are published for four years (1962—1965).

$\bar{x} = -2.4$ cm (Pallas is shorter)

$s = 4.2$

$t = 4.80^{***}$.

The difference between Pallas and Bonus is highly significant. Cf. further under (10). No indication of a variation between years.

(9) The analysis of variance gives the following results:

Yield (decitons/hectare)	Standard deviations: Between localities within years	Standard deviations: Between years
Pallas $\bar{x} = 49.55$	7.01°	6.18***
Bonus $\bar{x} = 48.57$	6.72°	5.99***
Lodging resistance		
Pallas $\bar{x} = 4.506$	2.28°	1.30***
Bonus $\bar{x} = 6.092$	2.35°	1.01***

There is no indication of a difference in the numerical values of variance (standard deviation) of Pallas and Bonus with regard to yield. The two sets of standard deviations are of the same magnitude both within and between years. The small excess of the Pallas values lacks significance and entirely disappears when the standard deviations are corrected to identical yield levels.

In the case of lodging resistance, on the other hand, Pallas shows a higher variance than Bonus between years, even when disregarding the different mean values of lodging. There is no difference between the varieties within years. Correcting, however, for the different mean values of lodging, the variance values of Pallas will be greatly accentuated and then become significant both between and within years. The interpretation is simple. The average lodging figure of Bonus (6.092) is definitely displaced to the lodging side, whereas the figure of Pallas (4.506) lies almost in the middle of complete erectness and complete lodging. Under the prevailing conditions on Zealand, therefore, Pallas will automatically have a greater potential of varying both to the extreme positive and the extreme negative side, whereas Bonus is more apt to vary to the negative side only. Under other climatic conditions, for instance with lodging figures displaced to the erect side, the variance will automatically turn higher for Bonus than for Pallas.

(10) In his computations of the land-wide comparisons of Pallas and Bonus THÖGERSEN has also recorded straw production. In the years of 1959 to 1963 (to select representative trials) he reported of grain yields in 301 trials and of corresponding straw yields in 194 trials. Pallas was superior in grain yield by 1.1 per cent, inferior in straw yield by 1.3 per cent. This means that the „generative efficiency" (DORMLING et al., 1966) is greater in Pallas than in Bonus, a fact also evidenced by the property of lower straw height in the case of Pallas (analysis 8 above). For every deciton of straw Bonus has produced 102 kilograms of grain. The corresponding productivity of Pallas amounts to 105 kilograms, i.e. three kilograms more.

The total yield (grain plus straw) is almost entirely similar for the two varieties (Pallas is inferior by less than 0.3 per cent; the difference is insignificant). This further elucidates the displacement of Pallas productivity towards the generative side.

The Zealand data favour the same conclusion.

Discussion and conclusions

It has frequently been argued that the value of the so-called mutation method in plant breeding has been overrated as a source of improved varieties. However, at the present time, some early evaluations of the method, for instance by GUSTAFSSON

(1942, p. 64; 1946, p. 341; 1947, pp. 87–92), and then in a more precise wording by GUSTAFSSON and TEDIN (1954, p. 636), seem to be valid, viz. that "the majority of high-productive mutants would not be suited for direct marketing.... The basic use of induced mutations would therefore ... consist in the accumulation of new materials for the continued recombination work along traditional lines". It is with this restriction the more interesting that induced mutants have in fact been released and that they constitute top-varieties on the market, also in species like barley with a very high breeding standard in Scandinavia. Mistakes and misunderstandings, put forward for instance by HUTCHINSON (1958) and DAVIES (1960), have been analysed and rejected in a publication by GUSTAFSSON (1963), to which the reader is referred.

The yield efficiency and agricultural behaviour of Pallas barley further clears some doubts of the usefulness of the mutation method. Pallas is a one-factor mutant in the locus ert-*k*. It implies a direct and definite improvement of its parent strain Bonus with regard to lodging resistance. In "specific yielding ability" (GUSTAFSSON, 1963, p. 221) it is, at least, equal to that of Bonus under conditions optimal to both parent and mutant. In fact, owing to its better lodging resistance, Pallas becomes higher yielding than Bonus in fertile soils, applying high nitrogen dressings. The biometrical treatment of Danish data has shown that there is in these two varieties a negative correlation between yield and lodging: the higher the lodging, the less the yield, and *vice versa*. Since Pallas is lodging resistant, this automatically causes a rise in its yield above the level of the more lodging susceptible Bonus. The over-all Zealand difference in yield by 2 per cent is statistically significant.

Another interesting fact deals with the yield variation of Pallas and Bonus within and between years. Contrary to a view put forward by ALLARD (1960, p. 445), misquoting FRÖIER (1954, p. 542), there is no indication of a higher degree of yield variation in Pallas than in Bonus. The standard deviations (variances) are almost exactly alike. With regard to lodging Pallas is more variable than Bonus but this does not depend on any agricultural short-coming of Pallas, rather on a displacement to the lodging side of the Bonus variety in the fertile Zealand soils.

Pallas has a lower straw height than Bonus, as well as a changed internode number and structure (EHRENBERG et al., 1956, Fig. 8). Its straw yield per hectare is less than that of Bonus. Since its grain yield is higher, this implies that per unit harvested straw of Pallas there is a surplus of grain as compared to Bonus, in fact per 100 kilograms of straw 105 kilograms of grain instead of 102 kilograms. This is an indication of a better "generative efficiency"; the waste of vegetative matter in grain production has become less than in the parent strain. In addition, Pallas has gained a better resistance to lodging and a higher absolute grain yield.

All in all: Pallas barley implies a definite improvement to its high-yielding parent strain Bonus. This does not imply that Pallas is a unique variety in all characters. In fact, since it is formed on the genetic "backbone" of Bonus, it has also received some weak features of the parent variety, *inter alia* a certain susceptibility to mildew, virus and nematode diseases, as well as to straw breakage at maturity, although, according to THÖGERSEN (1965, p. 98), "this condition has been of no importance for the yield of grain".

This is then where the second phase of the mutation method in plant breeding comes into action, that of gene recombination: implying an accentuation of good characters and a removal of inferior ones. The mutation giving rise to Pallas is simple in behaviour — in fact it acts like a one-factor change. Consequently, it is easy to handle in hybridization. Recent work at the Swedish Seed Association demonstrates that yielding ability and lodging resistance can be further accentuated, and that these important characters can be combined with mildew and nematode resistance, as well as a superior resistance to straw breakage and a high malting quality.

It is interesting to note that Pallas up to 1965 has surpassed every Swedish variety tested under Danish conditions. The conclusion is close at hand that it would even surpass these varieties in appropriate Swedish environments if tested and truly evaluated under adequate conditions.

Zusammenfassung

Die Gerstensorte Svalöfs Pallas geht auf eine im Jahre 1947 entstandene röntgeninduzierte *erectoides*-Mutante der ertragreichen Sorte Bonus zurück. Beide Sorten wurden von dem Schwedischen Saatzuchtverein in Svalöf gezüchtet. Nach eingehender Prüfung wurde sie 1958 als schwedische Zuchtsorte zugelassen und erlangte durch ihre gute Ertragsfähigkeit, die wesentlich verbesserte Standfestigkeit und gute Stickstoffverwertung weite Verbreitung in großen Teilen Westeuropas.

Die Ergebnisse der dänischen Gersten-Sortenprüfungen werden alljährlich veröffentlicht. 1958 wurde Pallas erstmalig in diese Versuche einbezogen, bei denen bis einschließlich 1964 ihre Ausgangssorte Bonus als offizielle Standardsorte diente. Sie wurde 1965 durch Pallas ersetzt. Beide Sorten wurden in bezug auf Ertragsfähigkeit, Standfestigkeit, Strohlänge und Strohertrag sorgfältigen biometrischen Prüfungen unterzogen, weiterhin wurden der Einfluß erhöhter Standfestigkeit auf die Ertragsfähigkeit untersucht sowie Ertrags- und Standfestigkeitsvarianzen geschätzt.

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Vergleichende Untersuchungen über die autotetraploiden Formen der Tomate*

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Comparative investigations on autotetraploid forms of the tomato

Summary. In experiments over some years observations were made on autotetraploid tomato lines involving *Lycopersicon peruvianum*, *L. pimpinellifolium*, five varieties of *L. esculentum* var. *cerasiforme* and var. *piriforme*, and six cultivated varieties, Resista, Aranyalma (Golden Apple), Bonny Best, Mikado, Bounty and San Marzano. The tetraploids of the self-incompatible *L. peruvianum* were not isogenic with the corresponding diploids and behaved inconsistently with the general trend of the autotetraploid lines in some instances.

The effect of tetraploidy on the cotyledons was to increase their width in all cases, their length in lines with relatively small cotyledons, but to reduce their length in lines with larger cotyledons. In agreement with the general features of the autotetraploids, however, the organs are wider and thicker than those of normal diploid plants. The width to length ratio was in all cases considerably higher in autotetraploid tomatoes than in diploids.

The fruit shape tended to be globular in all autotetraploid lines, their width-length index was higher than that of the diploid varieties with slightly elongated spherical or with elongated fruit and was lower than that of the corresponding diploids with flattened or oblate fruit. In neither case of the contrasting trends did it pass the value 1.00.

Tetraploidy was associated with increased pollen size and seed weight, and with reduced pollen viability (i.e. percentage of the stainable pollen grains), fruit weight and relative fertility (i.e. number of seeds per fruit); this agrees with data from publications on tomatoes.

Vor 50 Jahren hat H. WINKLER die erste experimentell erzeugte autotetraploide Pflanze in seinen klassischen Art-Pfropfungen zwischen *Lycopersicon* und *Solanum nigrum* erhalten. Seitdem sind von vielen Seiten autotetraploide Formen sehr verschiedener Tomatensorten und auch -arten, zuerst mit der verbesserten Dekapitierungsmethode von C. A. JÖRGENSEN und später fast ausschließlich mit der Colchicinmethode, hergestellt worden (RICK und BUTLER, 1956). Die Untersuchungen erstreckten sich in den meisten Fällen auf Vergleiche weniger Eigenschaften in autotetraploiden Formen von Kultursorten. Größere vergleichende Untersuchungen von primitiven Formen und Kultursorten der Tomate mit statistisch bearbeiteten Resultaten sind uns nicht bekannt. Diese Tatsache hat den Anlaß gegeben, die Ergebnisse unserer über mehrere Jahre durchgeführten Versuche mit Kultursorten und Primitivformen sowie Wildarten zusammenfassend darzulegen. Es ist bekannt, daß in der Regel die tetraploiden Formen von den diploiden mit großer Sicherheit unterschieden werden können, aber wegen der polygenen Bedingtheit der phaenotypischen Merkmale, die auch die statistische Bearbeitung der Daten erforderte, lassen sich die Unterschiede nicht leicht definieren (FABERGÉ, 1936).

Material und Methode

Für die Untersuchungen wurden 13 Sippen mit verschiedener Herkunft verwendet, deren Charakterisierung in der Arbeit von LEHMANN (1955) zu finden ist. L-21 ist eine Linie der Wildart *Lycopersicon peruvianum* (L.) Miller und L-4 eine Linie der primitiven Art *L. pimpinellifolium* (Jusl.) Miller. Von den 4 primitiven Formen von *L. esculentum* Miller convar. *parvibaccatum* Lehmann gehört die rotfrüchtige Sippe C-6 zu var. *cerasiforme* (Dunal) Alefeld, die rotfrüchtige Linie P-2 und die gelbfrüchtige P-11 sowie unsere gelbfrüchtige Selektion mit farbloser Fruchthaut (E-A) zu var. *piriforme* (Dunal) Alefeld; die fünfte primitive Form C-11 mit sehr stark gegabeltem Wickel ist eine Sippe aus der convar. *scopigerum* Lehmann. Die verwendeten 6 Kultursorten von *L. esculentum* vertreten 5 verschiedene Provarietäten der convar. *infiniens* Lehmann, und zwar 'Aranyalma' (Goldener Apfel, E-13) die Provar. *flammatum* Lehmann, 'Resista' (E-12)

* Herrn Professor Dr. HANS STUBBE zum 65. Geburtstag gewidmet.