A DWARF MUTATION IN PORTULACA SHOWING VEGETATIVE REVERSIONS¹

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TABLE OF CONTENTS

Dwarf plants	419
Description of dwarfs	420
Inheritance of dwarf habit	421
Vegetative reversions	424
Frequency of occurrence of reversions	424
Genetic constitution of reverting branches	426
DISCUSSION OF RESULTS	430
SUMMARY	433
LITERATURE CITED	433

DWARF PLANTS

In 1914 Mr. B. T. AVERY, who was then my gardener assistant at the CONNECTICUT AGRICULTURAL COLLEGE, called my attention to a single dwarf individual in a bed of red-flowered plants from commercial seed of a variety of *Portulaca grandiflora*. This plant formed a low compact pin-cushion-like growth in striking contrast to the long straggling habit of the normal plants near it. It is the origin of a series of dwarfs which we now have in a variety of colors, both singles and doubles. Commercial florists are on the lookout for dwarf plants for bedding purposes and such a cushion form as ours would likely have been noticed and propagated commercially by trained florists. So far as we have been able to ascertain, however, no dwarf form of *Portulaca* is known to the trade. It is not unlikely, therefore, that the plant discovered by us was the first of its kind to be observed in this species.

¹ A preliminary report on the present paper may be found under BLAKESLEE, A. F., and AVERY, B. T., Jr., A vegetative reversion in *Portulaca*. Brooklyn Bot. Garden Mem. 1: 18. 1918.

Description of dwarfs

Figure 1, at the right, shows two typical young dwarfs in 3-inch pots, in contrast to a normal plant of the same age at the extreme left. Dwarfing is brought about by an inhibition to the normal elongation of the internodes. Branching does not seem to be interfered with, and older plants may form dense mats 4 inches and more in diameter.

In normal plants, red in the stem is correlated with red and certain other colors in the flower. Typical dwarf plants in the adult stage, however, always have green stems. In young seedlings, both normals

FIGURE 1.—*Portulaca*. Normal, dwarfs and dwarf reverting to normal

and dwarfs have similar primary stems, of a red color if destined to produce flowers correlated with red stems. Dwarfs beyond the seedling stage have no red in their stems. It was at first thought that their lack of color might be caused by the dense covering of leaves which kept out sufficient light to stimulate the production of the red color. Lack of illumination is not the only factor involved however, since stripping a dwarf stem of its leaves and removing them from the branch as soon as formed does not elicit red stem color in dwarfs even in direct sunlight. Moreover, reverting branches, to be discussed later, have red stems and often show a sharp line of color where they arise from a dwarf branch. It appears therefore that there is something peculiar in the make-up of

the dwarf plant which inhibits color in its stem though not inhibiting color in its flowers.

Occasionally in the offspring of dwarfs, a few individuals have appeared of an intermediate type which have been called "tall dwarfs." These have pale stems for the most part and longer internodes than typical dwarfs but are not to be confused with normals. Their inheritance has not been investigated in crosses but so far as tested they breed true to the intermediate character when selfed.

Inheritance of dwarf habit

In inheritance the dwarf habit is transmitted as a simple Mendelian recessive. Table 1 shows the result of selfing dwarf plants. All of the 2653 offspring thus obtained are dwarfs with the exception of 14 individuals (0.5 percent) which are normals. These exceptions in cases where the flowers were unguarded against insect visitation might be attributed to chance out-crossing. It seems likely that these as well as the others may better be accounted for by reversions to be discussed later. The normal plant in pedigree 16149 was found to be heterozygous, giving when selfed 29 normals to 15 dwarfs, a fact which would be expected with the assumption of either out-crossing or reversion, but would be less likely from a chance mixture of seed. The unguarded plants listed in these tables were grown in a screened greenhouse and, probably for this reason, gave little evidence of out-crossing when unguarded.

Table 2 shows the result of pollinating normals by dwarfs and the reciprocals. All the offspring are normal. In table 3 are given the numbers of normals and dwarfs in the F_2 offspring. The numbers fail to show a perfect 3 to 1 ratio, being more nearly in the proportion of 4:1. The fact that, in general, mutants tend to be less viable than normals, might account for the reduced number of dwarfs in the F_2 pedigrees. Individual pedigrees however show a considerable variation from expectation.

Table 4 includes the offspring of the F_1 plants back-crossed to the recessive dwarf type. Here again the individual pedigrees are not all as should be expected. Although the two with small numbers can be classed as 1:1 ratios the other two with larger numbers appear to form more nearly a 2:1 ratio. It is probably a curious coincidence only that the two F_1 plants, 16124 (5) and 1692 (4), which when back-crossed gave good 1:1 ratios, gave when selfed, ratios of roughly 4:1 and 9:1 (cf. table 3). This latter pedigree showed the greatest departure from a 3:1 ratio of any in the table.

TABLE I
Dwarf plants selfed

Record year	Pedigree number	Parent	Pollination	Normal	Dwarf
1916	1560	13206	Guarded		72
1917	16120	1560 (61)	Guarded	I	50
	16123	1560 (63)	Guarded		23
	16130	1560 (64)	Guarded		6
	16134	1560 (64)	Guarded		11
	16135	1560 (65)	Guarded		61
	16137	1560 (65)	Guarded		18
	16140	1560 (65)	Guarded		85
	16145	1560 (70)	Guarded		25
	16147	1560 (71)	Guarded		24
	16149	1560 (72)	Guarded		32
	16152	1560 (74)	Guarded		17
	16157	1560 (78)	Guarded		41
	16160	1560 (79)	Guarded		37
	16165	1560 (126)	Guarded		52
	16170	1560 (126)	Guarded		40
	16178	1560 (138)	Guarded		26
	16184	1560 (140)	Guarded		31
	16191	1560 (142)	Guarded		41
	16205	1560 (145)	Guarded		46
	16220	1560 (172)	Guarded		70
1918	1764	16120 (1)	Unguarded	I	37
	1768	16120 (4)	Unguarded	I	85
	1793	16123 (2)	Guarded		37
	1794	16123 (3)	Guarded		61
	1795	16123 (3)	Unguarded		54
	1769	16140 (1)	Unguarded		90
	1770	16140 (2)	Unguarded		44
	1773	16140 (4)	Unguarded	I	146
	1792	16181 (3)	Unguarded		30
	1796	16205 (2)	Unguarded	I	127
	1797	16205 (3)	Unguarded	I	57
1919	1899	16140 (5)	Unguarded	I	40
	1898	16165 (3)	Unguarded		394
	1890	1742 (3)	Guarded		18
	1892	1742 (7)	Guarded		3
	184	1744 (3)	Guarded		23
	1895	1745 (4)	Guarded		29
	1851	1746 (4)	Guarded		7
	1852	1746 (5)	Guarded		17
	1853	1746 (6)	Guarded		9
	1875	1749 (1)	Guarded		12
	1876	1749 (2)	Guarded		9
	1897	1751 (3)	Guarded		204
	18102	1752 (2)	Guarded		196
	18103	1757 (1)	Guarded		43
	18104	1758 (1)	Guarded		43
	18105	1759 (1)	Guarded		30
Totals—Guarded capsules only.				9	1549
Unguarded capsules only.				5	1104
Guarded and unguarded capsules.				14	2653

TABLE 2
(Normal $\times$ dwarf) F_1

Cross	Number of pedigrees			Normals	Dwarfs
	1917	1918	1919		
Normals $\times$ dwarfs	23	2	1	590	0
Dwarfs $\times$ normals	6			112	0
Totals	29	2	1	702	0

TABLE 3
(Normal $\times$ dwarf) F_2

Pedigree number	Parent	Pollination	Original cross Dwarf $\times$ normal		Original cross Normal $\times$ dwarf		Grand totals	
			Normal	Dwarf	Normal	Dwarf	Normal	Dwarf
1742	16124 (2)	Unguarded	77	22				
1743	16124 (5)	Unguarded	82	22				
1744	16146 (2)	Unguarded	25	14				
1745	16148 (2)	Guarded	99	21				
1746	1625 (4)	Guarded			63	15		
1747	1652 (2)	Unguarded			34	13		
1750	1693 (4)	Unguarded			89	13		
1749	16104 (2)	Guarded			48	15		
1866	1692 (4)	Guarded			94	10		
1842	1738 (1)	Guarded			95	21		
1849	1740 (1)	Guarded			81	28		
1850	1740 (2)	Guarded			90	18		
1886	1741 (1)	Guarded			78	19		
Totals—Guarded capsules only...			99	21	549	126	648	147 $\pm$ 8.23
Unguarded capsules only...			184	58	123	26	307	84 $\pm$ 5.77
Guarded and unguarded capsules			283	79 $\pm$ 5.56	672	152 $\pm$ 8.38	955	231 $\pm$ 10.06
Calculated ratios			271.5	90.5	618	206	889.5	296.5

TABLE 4
 $F_1 \times$ dwarf recessive

Pedigree number	Parent	(Dwarf $\times$ normal) $F_1 \times$ dwarf		(Normal $\times$ dwarf) $F_1 \times$ dwarf		Totals	
		Normal	Dwarf	Normal	Dwarf	Normal	Dwarf
1758	1625 (5) $\times$ 1560 (72)			44	23 $\pm$ 2.76		
1759	1692 (4) $\times$ 1560 (76)			9	7 $\pm$ 1.35		
1756	16124 (5) $\times$ 1560 (76)	15	15 $\pm$ 1.85				
1757	16159 (6) $\times$ 1560 (60)	25	10 $\pm$ 1.69				
Totals		40	25 $\pm$ 2.72	53	30 $\pm$ 3.07	93	55 $\pm$ 4.10
Calculated ratios		32.5	32.5	41.5	41.5	74	74

From the foregoing tabulations one would feel satisfied in concluding that the dwarf character in *Portulaca* is a simple Mendelian character recessive to the dominant normal habit of growth. Recessive characters when they appear should be homozygous for their determining factors and in consequence dwarfs when selfed should give rise only to dwarfs and never to normal plants. The number of exceptions in our cultures (0.5 percent) though small, we cannot believe were due entirely to experimental errors. Their significance may be clearer after a discussion of the phenomenon of vegetative reversions.

VEGETATIVE REVERSIONS

The most interesting peculiarity of the mutant under discussion is the fact that some of the dwarf plants give rise to branches normal in appearance. Such a reverting dwarf is shown in figure 1. The reverting branches have long internodes and red stems and are otherwise indistinguishable in appearance from pure normals.

Frequency of occurrence of reversions

Reverting branches may occur apparently at any stage in the development of the plant. They have been found occurring late in the season on large dwarf plants and also at so early a stage that the specimen would have been classified as a normal if the small dwarf axis had not been discovered at the base of the plant. It seems best in computing their frequency to take into consideration only a series that was sown and kept under observation for this purpose. The pedigrees in table 5 were grown to discover if increasing the amount of bone meal in the nutrient would increase or decrease the frequency of reverting branches. No effect of the treatment upon the occurrence of reverting branches could be observed. The data accordingly can be combined as shown in table 6 to give the proportion of dwarfs with reverting branches (called "reverters") to typical dwarfs. Of the 1294 dwarfs in this table, 16, or 1.23 percent, were reverters. Reverters have been classed with dwarfs in table 6 as in previous tables. The proportion of reverters and of normals is higher in certain pedigrees than in others. The data are not sufficient however to indicate whether an increased tendency toward reversions and normals actually exists in these cases. Reversion may probably take place at any stage in the development of the zygote. It might even be expected at the formation of the gametes. If this is true we

TABLE 5
Dwarf plants selfed, reverter test

Pedigree number	Parent	Pollination		Pure sand	Sand	Soil	Soil + 50	Soil + 100	Soil + 150	Soil + 200	Soil + 250	Soil + 300	Soil + 400	Soil + 500	Total, A-K incl.
				A	B	C	D	E	F	G	H	I	J	K	
True dwarfs 1897	1751 (3)	Guarded	Dwf Rev Nor dd	20	19	19	19	19	19	20	20	20	17	10	202
						1		1	1				1		2
					1										3
													2		3
1898	16165 (3)	Unguarded	Dwf Rev Nor dd	40	40	39	39	38	38	38	40	32	29	16	389
									1	1		1		2	5
						1	1	2	1	1		7	11	22	46
					15	15								10	40
1899	16140 (5)	Unguarded	Dwf Rev Nor dd												
18102	1752 (2)	Guarded	Dwf Rev Nor dd	19	18	16	18	20	18	19	20	20	14	6	188
					2	1	1		2	1			1		8
				1		1	1						1		4
						2							4	14	20
18103	1757 (1)	Guarded	Dwf Rev Nor dd		15	15								13	43
18104	1758 (1)	Guarded	Dwf Rev Nor dd		14	15								13	42
					1										1
18105	1759 (1)	Guarded	Dwf Rev Nor dd		10	10								10	30
Tall dwarfs 1896	16123 (6)	Guarded	Dwf Rev Nor dd	20	20	20	20	20	20	20	19	10			169
											1				1
18100	1743 (1)	Guarded	Dwf Rev Nor dd		20	20		20		20		20			100
18101	1743 (2)	Guarded	Dwf Rev Nor dd		25	25								25	75

Explanation.—The plants were grown in different substrata indicated by letters in heading. A is sand cleaned and watered with distilled water. B is sand watered with tap water. C is potting soil. D to K is potting soil plus bone meal. In each case the amounts of bone meal in grams noted in the table were added to about 6 kilos of soil. Dead, unrecordable plants are listed as "dd."

should expect plants that have reverted at or before the seedling stage to be indistinguishable in appearance from normals. Normals in these pedigrees therefore may be considered as early reverters. If so and we include the 7 normals with the 16 obvious reverters of table 6 we have 23 reversions out of 1301 plants or 1.77 percent.

TABLE 6
Dwarf plants selfed; reverter test

Pedigree number	Parent	Pollination	Dwarf	Reverter	Normal	Total
1897	1751 (3)	Guarded	202	2	3	207
1898	16165 (3)	Unguarded	389	5		394
1899	16140 (5)	Unguarded	40			40
18102	1752 (2)	Guarded	188	8	4	200
18103	1757 (1)	Guarded	43			43
18104	1758 (1)	Guarded	42	1		43
18105	1759 (1)	Guarded	30			30
1896	16123 (6)	Guarded	169			169
18100	1743 (1)	Guarded	100			100
18101	1743 (2)	Guarded	75			75
Total plants recorded			1278	16	7	1301
Percents			98.23	1.23	0.54	100.00

Genetic constitution of reverting branches

The genetic constitution of reverting branches can be discovered (1) by selfing individual flowers of reverting branches, and (2) by back-crossing them to typical dwarfs and normals.

The result of selfing flowers from reverting branches is shown in table 7. A summary of dwarfs and normals in the offspring shows a close agreement with a 3:1 ratio and indicates that the reverting branch is heterozygous for the dwarf character. The first two figures in the pedigree number represent the year in which the seed was harvested. It will be noted that pedigrees 16128, 16181, and 16186 are from the same plants respectively as 1778, 1780, and 1781. These latter pedigrees were from cuttings from reverting branches, rooted and kept growing to the second year. The three reverting branches of these plants selfed in 1916 gave a ratio of 95:20 which in numbers per 4 is $3.30:0.70 \pm 0.109$ with a difference from the expectation of 2.75 times its probable error, while cuttings from the same reverting branches a year later gave a ratio of 255:75 which in numbers per 4 is $3.09:0.91 \pm 0.064$ with a difference from

expectation of only 1.41 times its probable error. We may conclude in consequence that in their growth for upwards of a year these reverting branches had not undergone any change that would increase their tendency to throw normals.

TABLE 7
Reverting branches selfed

Pedigree number	Parent	Pollination	Reverting branch	
			Normal	Dwarf
16128	1560 (64)	Guarded	26	4
16181	1560 (138)	Guarded	15	2
16186	1560 (140)	Guarded	54	14
16193	1560 (142)	Guarded	59	19
16199	1560 (142)	Guarded	46	9
16206	1560 (145)	Guarded	34	6
16208	1560 (145)	Guarded	25	20
16210	1560 (145)	Guarded	50	16
1760	16120 (1)	Guarded	84	37
1761	16120 (1)	Unguarded	66	24
1762	16120 (1)	Unguarded	35	9
1765	16120 (2)	Unguarded	25	6
1767	16120 (4)	Unguarded	16	6
1771	16140 (2)	Guarded	61	27
1772	16140 (2)	Unguarded	53	17
1774	16140 (4)	Guarded	48	12
1775	16165 (1)	Guarded	32	5
1776	16165 (1)	Unguarded	104	38
1778	1560 (64)	Unguarded	91	30
1780	1560 (138)	Unguarded	95	14
1781	1560 (140)	Unguarded	69	31
1791	16181 (3)	Unguarded	146	36
Total—Guarded capsules only.....			534	171± 7.75
Unguarded capsules only.....			700	211± 8.81
Guarded and unguarded capsules.....			1234	382± 11.74
<i>Calculated values</i>			1212	404

In table 8 are summarized the results of selfing reverting branches and dwarf branches from the same plants. The dwarf branches breed true to the dwarf character to the same extent shown by dwarf plants that have not reverted. It is for this reason that dwarf branches of reverters have been included in table 1.

The normal plants obtained by selfing reverting branches have themselves been tested by being selfed, with the results shown in table 9 (A).

TABLE 8
Reverting branches and dwarf branches from same plant selfed

Parent	Reverting branch		Dwarf branch	
	Normal	Dwarf	Normal	Dwarf
1560 (64)	117	34	0	17
1560 (138)	110	16	0	26
1560 (140)	123	45	0	31
1560 (142)	105	28	0	41
1560 (145)	109	42	0	46
16120 (1)	185	70	1	37
16120 (4)	16	6	1	85
16140 (2)	114	44	0	44
16140 (4)	48	12	1	146
16181 (3)	146	36	0	30
Totals.....	1073	333±10.95	3	503
Calculated values.....	1054.5	351.5		

TABLE 9
(A) Normals from reverting branch selfed

Pedigree number	Parent	Pollination	Segregating pedigrees		Uniform pedigrees	
			Normal	Dwarf	Normal	Dwarf
1782	16128 (1)	Guarded	79	12		
1783	16128 (2)	Guarded	43	13		
1784	16128 (3)	Guarded	101	18		
1789	16181 (1)	Guarded	37	5		
1790	16181 (2)	Unguarded	45	24		
1785	16186 (1)	Guarded			33	0
1786	16186 (2)	Guarded	38	11		
1787	16186 (3)	Unguarded	162	50		
1788	16186 (4)	Unguarded	130	34		
Totals—Guarded capsules only.....			298	59	33	0
Unguarded capsules only.....			337	108		
Guarded and unguarded capsules.....			635	167±8.27	33	0
Calculated values.....			601.5	200.5		

(B) (Normal × reverting branch) F₂

1753	162 (2)	Guarded			74	0
1754	162 (3)	Guarded	83	17		
1755	1648 (1)	Unguarded			72	0
1751	16102 (4)	Unguarded	68	13		
1752	16114 (1)	Unguarded	112	19		
Totals—Guarded capsules only.....			83	17	74	0
Unguarded capsules only.....			180	32	72	0
Guarded and unguarded capsules.....			263	49±5.17	146	0
Calculated values.....			234.75	78.25		

One would expect more of these normals to be heterozygous than homozygous for the normal character. This expectation is realized, although not in the exact proportion of two heterozygous to one homozygous individual which a larger series of tests might more nearly approximate.

The second method of testing the genetic constitution of reverting branches is to cross them with each member of the allelomorphic pair. In all, 10 pedigrees were secured by crossing reverting branches with dominant normals. The 309 offspring in the F_1 generation were all normals. The expectation is that half of the normals would be homozygous normals and half would be normals heterozygous for dwarfing. This expectation is well satisfied as shown in table 9 (B), inasmuch as three are segregating pedigrees and two are uniform.

TABLE 10
Reverting branch $\times$ dwarf recessive

Pedigree number	Parents	Normal	Dwarf
16131	1560 (64) $\times$ 1560 (64)	1	1
16132	1560 (64) $\times$ 1560 (64)	3	0
16190	1560 (142) $\times$ 1560 (142)	4	9
1763	16120 (1) $\times$ 1560 (76)	22	19
1766	16120 (2) $\times$ 1560 (76)	10	6
1777	1560 (64) $\times$ 1560 (72)	41	46
1779	1560 (64) $\times$ 1560 (72)	7	9
Totals		88	90 $\pm$ 4.50
Calculated values		89	89

A more convenient method of testing is to back-cross with the recessive dwarfs. The results are shown in table 10. The expectation of a 1:1 ratio is satisfied in that in the offspring 88 normals were obtained to 90 dwarfs. In all the crosses the reverting branches were used as the seed parents except 16131 which is the reciprocal of 16132. These two pedigrees and 16190 are crosses between reverting and dwarf branches of the same plant.

In table 11 are given summaries of the 1918 field tests of reverting branches of 3 plants which were both selfed and crossed with the dwarf recessive. This detailed analysis leaves no doubt that reverting branches are dominants heterozygous for the recessive factor.

TABLE 11
Reverting branch selfed and back-crossed to dwarf

Pedigree numbers	Parent	Reverting branch selfed		Reverting branch $\times$ dwarf	
		Normal	Dwarf	Normal	Dwarf
1760, 1761, 1762	16120 (1)	185	70		
1763	16120 (1) $\times$ 1560 (76)			22	19
1765	16120 (2)	25	6		
1766	16120 (2) $\times$ 1560 (76)			10	6
1778	1560 (64)	91	30		
1777 and 1779	1560 (64) $\times$ 1560 (72)			48	55
Totals		301	106 $\pm$ 5.89	80	80 $\pm$ 4.26
Calculated values		305.25	101.75	80	80

DISCUSSION OF RESULTS

The dwarf mutant of *Portulaca* is not peculiar in its inheritance. Like many dwarfs it is a recessive character. Like many other recessive mutants, the number of dwarfs runs somewhat below expectation in the F_2 generation. The chief interest in this form lies in the production of branches with the dominant habit of growth on otherwise recessive plants. Such reverting branches come under the category of bud sports or vegetative mutations. The appearance of bud variations is not a rare phenomenon in *Portulaca*, many of them being apparently in the nature of sectorial chimeras. The mutation responsible for the reverting branches apparently affects a single one of the paired recessive genes, changing it to the dominant allelomorph. In consequence the branch is heterozygous. This was the case in the dozen mutant branches tested, as shown in table 7. Extensive tests might ultimately discover a reverting branch homozygous for the dominant character. Such a condition would be expected, however, only after both of the recessive genes for dwarfing had reverted to normal, either simultaneously, or at different stages in development. Since heterozygous and homozygous branches are alike in appearance, their distinction can only be made by a breeding test. It seems not improbable that any single cell of the dwarf plant is liable to mutate to normal in one of the two paired genes. It is difficult to calculate what percentage of the dwarf cells mutate in this manner. If the 0.5 percent normals appearing in dwarf pedigrees could be assumed to come from mutating gametes we might calculate that 0.5 percent of the zygotes had the mutant gene or that 0.25 percent of the gametes them-

selves had mutated. Such an assumption, however, appears unwarranted since it is probable that some of the normals in dwarf pedigrees are to be considered reversions that have taken place at an early seedling stage. However, it can be assumed that certainly not over 0.25 percent or 1 in 400 of the gametes are liable to mutate. The percentage of mutated gametes is probably much smaller.

It may seem strange that the mutations from dwarf to normal seems relatively common while the reverse mutation, from normal to dwarf, has not been observed aside from our original dwarf of 1914. This fact might lead to the conclusion that mutation from a recessive to a dominant gene in this specific instance is more frequent than the mutation from the dominant to the recessive member of the pair. A brief consideration will show that such a conclusion would not be warranted from the data at hand. To be evident, dwarf mutations would have to exist in the homozygous (*aa*) condition. Using our figures above and assuming that the genes for normal mutate to dwarf as often as those for dwarf mutate to normal, viz., once in 400 times, in the formation of the gametes, we should require 400 times 400 or 160,000 gametes in order to have a single chance of obtaining a zygote with both determiners for dwarfing. One at the most out of some 80,000 offspring of selfed normal plants therefore should be dwarf (*aa*), and one at the most out of 200 normal plants should be heterozygous (*Aa*) and when selfed throw a 3:1 ratio of normals and dwarfs. Moreover, 1 out of 400 plants from the cross of normal by dwarf shown in table 2 should be dwarf, on this assumption. We have grown over 5300 offspring from lines with normal habit, including 109 selfed parents and 702 offspring from the cross of normal by dwarf and have never seen dwarf plants in the species, except those which could be traced back to the dwarf mutant found in 1914.

In table 12 are tabulated the chances (C) for the appearance of dominant and recessive mutations corresponding to various percentages (P) of mutated gametes. Formulae are given and their application shown by a few examples. In our figures above we assumed that all the 0.5 percent normals which appeared in dwarf pedigrees came from mutations in 0.25 percent of the gametes. The figure would probably still be much too high if it were a fifth as large or 0.05 percent. On the latter assumption, dwarfs would be expected to appear only once in 2,000,000 times from mutations in the gametes alone. Whatever figure is taken, it is obvious from the table that even though the appearance of a dominant mutant may be relatively common, the opposite recessive mutant will be found extremely rare although the mutations in the individual chromosomes may be equally frequent in the two directions.

If vegetative mutation from normals to dwarfs occurred with any frequency, they might be expected to appear as bud sports on heterozygous normal plants or on reverting branches. They have been looked for in the large number of heterozygous normals in our pedigrees but have not been discovered. Due to their slowness of growth, however, it is doubtful if they would have an opportunity of showing themselves even if such mutative changes should take place in the vegetative tissues involving a bud. A short dwarf branch on a vigorous normal plant would likely escape notice. Moreover, it is likely that a dwarf mutant bud would be entirely prevented from growing by the development of the more vigorous normal buds. So far as the obvious evidence goes, mutations from

TABLE 12

Percentage of mutant gametes	Chances of heterozygous mutant (<i>Aa</i>) from <i>AA</i> or <i>aa</i> selfed	Chances of homozygous mutant (<i>AA</i> or <i>aa</i>) from cross (<i>AA</i> × <i>aa</i>)	Chances of <i>AA</i> mutant from <i>aa</i> , or <i>aa</i> mutant from <i>AA</i>
P	$C = 1:\frac{50}{P}$	$C = 1:\frac{100}{P}$	$C = 1:\frac{5,000}{P^2}$
0.25	1:200	1:400	1:80,000
0.125	1:400	1:800	1:320,000
0.05	1:1,000	1:2,000	1:2,000,000
0.025	1:2,000	1:4,000	1:8,000,000

the recessive dwarf to the dominant normal condition is not extremely rare in this species while the mutation from the dominant normal to the recessive dwarf is a phenomenon that has been observed only once.

It is not our purpose at the present time to enter into any detailed discussion of the subject of vegetative mutations in *Portulaca*. EAST's (1917) paper on bud variations may be referred to in passing. It is agreed that bud variations come more frequently in hybrids due probably to the fact that in heterozygotes a mutation in only a single gene would be required for the appearance of a recessive which is the commonest type of vegetative mutations. The fact that the mutation under observation takes place with apparent frequency in one direction and not in the other may be due in part to the chances against the appearance of both the recessive genes in the same zygote.

SUMMARY

1. A dwarf mutation of *Portulaca grandiflora*, characterized by short internodes, is described and figured.
2. The dwarf habit of growth is inherited as a simple Mendelian character recessive to the dominant normal habit.
3. About 1.25 percent of the recessive dwarf plants produce reverting branches with the dominant normal habit of growth.
4. Occasional normals found in offspring of selfed dwarfs are probably due to reversions bringing about normal gametes or to reversions in the early development of the zygote.
5. Dwarf branches from reverting plants when selfed breed as true as typical dwarfs.
6. Reverting branches from otherwise dwarf plants are heterozygous and give 3:1 ratios, when selfed, and 1:1 ratios, when back-crossed to dwarfs.
7. The reverting branches produced by dwarfs are classed as dominant vegetative mutations.

LITERATURE CITED

- EAST, E. M., 1917 The bearing of some general biological facts on bud-variation. *Amer. Nat.* 51: 129-143.