necessary loss in yield. The trees with 30% foliage removed (30 AT) were underpruned. The slow recovery and generally poor performance of these trees indicated that this treatment is probably the least desirable commercially.

It can not be concluded that removing 50% of the canopy will always be the optimum treatment; however, it is a reasonable starting point. Adjustments could be made by taking into consideration other potentially important factors not included in this study, for example, tree age and rootstock. If trees younger than those used here were transplanted, then a larger part of the root system would be enclosed by the digger and proportionately less of the canopy would need to be pruned. Trees on different rootstocks vary in root distribution and vigor (4, 5, 6, 9), characteristics which could affect the rate of root regeneration as well as canopy regrowth.

In summary, 8-year-old 'Murcott' trees on rough lemon were transplanted successfully with a mechanical tree digger. The amount of foliage removed prior to transplanting had a significant effect on yield for a period of 4 years after transplanting, with 50% canopy removal being the best treatment. Application of an antitranspirant, and root pruning, did not provide any short- or long-term benefit.

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Inheritance, Linkage, and Gene Interaction Studies in Lettuce

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Abstract. **Two new lettuce genes are described and named: *chlorophyll deficient-2* (*cd-2*) and *Early flowering* (*Ef*). Brown pericarp is either a pleiotropic effect of *plump involucre* (*pl*) or is caused by a closely linked gene. *White pericarp* (*w*) is epistatic to brown. *Endive-like leaf* (*en*) and *white pericarp* are linked, with $P = 0.47$. *Virescent* (*vi*) and *fringe* (*fr*) are linked, with a recombination value of $p = 0.25$. Genes for spininess and anthocyanin color are linked. *Endive*, *white*, *virescent*, *fringe*, and *male sterile-6* (*ms-6*) form a linkage group. Three other double recessives have interactive relationships. *Endive* and *fringe* together are phenotypically extreme endive; *virescent* and *golden* (*go*) together are golden; *golden* and *chlorophyll deficient-2* are golden and partially lethal.**

The progress of research on the genetics of lettuce and related *Lactuca* species is summarized in a review paper by Robinson et al. (5), which describes the 59 major genes and 7 linked pairs identified to date. It also lists recommended rules of nomenclature and name and symbol changes to conform to those rules. The present paper adds 2 new genes and 3 linkages to the list, clarifies the genetic map, and discusses 5 interactive relationships.

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Materials and Methods

All genetic studies were conducted in the greenhouse. Plants were grown in plastic pots or flats as seedlings and transplanted to small plastic pots (8.25 or 10.16 cm^2) for observation of characters.

Table 1. Inheritance of chlorophyll deficiency in crosses with 72-473; expected numbers in parentheses.

Segregation	Population	Normal	Deficient	χ^2 (3:1)	P
F_2	71-318 x 72-473	533(537)	183(179)	0.12	0.7–0.8
	72-473 x Vanguard	441(450)	159(150)	0.72	0.3–0.5
	72-473 x 72-175	344(358)	134(120)	2.18	0.1–0.2
	6583 fr x 72-473	270(275)	97(92)	0.36	0.5–0.7
	72-473 x Jade *pl*	583(574)	182(191)	0.59	0.3–0.5
	Calmar *ms* x 72-473	666(675)	234(225)	0.48	0.3–0.5
	Total	1638(1657)	572(553)	0.87	0.3–0.5
F_3 families		*Among families*			
		Normal	Seg.	χ^2 (1:2)	P
	72-473 x Jade *pl*	190(176)	339(353)	1.67	0.1–0.2
		Within segregating families			
		Normal	Deficient	χ^2 (3:1)	P
	72-473 x Jade *pl*	5194(5064)	1559(1689)	13.34	<0.01

Crosses were made by the method of Oliver (4), modified to maximize the number of hybrid seeds. The lettuce flower consists of a style with a 2-part stigma enclosed in a tube formed by fused anthers. These shed pollen on the inside surface as the style elongates. Oliver's method consists of washing the pollen off the exposed stigmas at a specific stage of elongation. This was modified by washing before, during, and after the critical stage and resulted in a higher proportion of hybrids.

Genetic ratios were compared by standard chi square procedure. One or both gene segregations in a few linkage tests were disturbed and linkage χ^2 was calculated with marginal totals. Maximum likelihood tables were used to calculate recombination values (1). Recombination values are denoted by "p" and probability values by "*P*".

Inheritance studies

Chlorophyll deficiency. In 1971, I found a plant with yellowed leaves in a commercial planting of 'Calmar' in the Salinas Valley. It was designated 72-473, transplanted into the greenhouse and crossed with 6 normal green parents: 'Vanguard', breeding line 72-175, and 4 mutant lines [71-318 (*endive-like leaf*), Calmar *ms* (*male sterile-6*), 6583 *fr* (*fringe leaf*), and Jade *pl* (*plump involucre*)]. All F_1 plants were normal green, indicating that green is dominant.

All F_2 populations segregated 3 normal : 1 chlorophyll deficient, signifying a single gene (Table 1). F_3 families were grown from green F_2 plants of the cross 72-473 x Jade pl. Families were normal green or segregating, in the ratio 1:2, as expected.

Table 2. Inheritance of chlorophyll deficiency in the cross M648-2 x Salinas; expected numbers in parentheses.

Populations	Distribution (expected) Normal	Segregating	Chlor. def.	χ^2	P
F_2 (expect 3:1)	68(71)	---	27(24)	0.51	0.3–0.5
Among F_3 families (expect 1:2:1)	22(23.75)	46(47.5)	27(23.75)	0.62	0.7–0.8
Within segregating F_3 families (expect 3:1)	342(351)	---	126(117)	0.92	0.3–0.5

However, within segregating families, there was a highly significant shortage of chlorophyll-deficient plants.

It was postulated that there may be some difficulty in distinguishing normal from deficient plants under certain circumstances. The plants were first counted in the seedling stage. In a group of 19 segregating F_3 families, the count was: 273 normal, 46 chlorophyll-deficient (χ^2 (3:1) = 19.28, $P < 0.01$). Twelve plants were randomly selected from each family and transplanted, one plant per pot. A later count among the transplants was: 173 normal, 52 chlorophyll-deficient (χ^2 = 0.37, P = 0.5–0.7).

In a 2nd group of families, recounts of plants still in the seedling pots were made by a 2nd person. The first count was: 199 normal, 34 chlorophyll-deficient (χ^2 = 13.22, $P < 0.01$) and the second count: 174 normal, 59 chlorophyll-deficient (χ^2 = 0.03, P = 0.8–0.9). Therefore, the problem was probably either the time of observation, the condition of the plants, the person counting or some combination of these. Overall, the data support the hypothesis of a single gene, with chlorophyll deficiency recessive.

In 1977, several yellow-green plants were noted in progeny M648-2, which was being tested for resistance to lettuce mosaic. The cross M648-2 x 'Salinas' was made. The F_1 was normal green and the F_2 segregated 68 normal : 27 chlorophyll-deficient (Table 2), indicating a single gene, with normal dominant to chlorophyll-deficient. F_3 family segregation confirmed the single gene inheritance (Table 2).

The appearance of the chlorophyll-deficient plants in 72-473 and in M648-2 was similar. They were crossed reciprocally, and with R-34, a chlorophyll-deficient line reported earlier (8).

The F_1s from R34 x M648-2 and R34 x 72-473 were both green; R34 (*cd*) is therefore different from the other 2. [New

Table 3. Inheritance of early flowering in lettuce, F_2 populations; expected number in parentheses.

Populations	Distribution (expected) Early	Late	χ^2 (3:1)	P
56679E x Vanguard 75(A)	71(70.5)	23(23.5)	0.01	0.9–0.95
56679E x Vanguard 75(B)	73(71.25)	22(23.75)	0.16	0.5–0.7
56679E x Vanguard 75(C)	25(25.5)	9(8.5)	0.04	0.8–0.9
56679E x Salinas(A)	36(35.25)	11(11.75)	0.07	0.7–0.8

Table 4. Mean flowering times for early and late flowering classes. Number of days from seeding to first open flower.

Populations	Mean flowering time (days) Early	Late
56679E x Vanguard 75(A)	62	126
56679E x Vanguard 75(B)	63	124
56679E x Vanguard 75(C)	50	111
56679E x Salinas(A)	59	139
56679E x Salinas(B)	---	131
Mean	60	118

Table 5. Inheritance of early flowering in lettuce, F_3 families.

Population: 56679E x	Observed (expected) Early	Segr.	Late	χ^2	P
Segregation among families				*1:2:1*	
Vanguard 75(A)	26(23.25)	44(46.5)	23(23.25)	0.46	0.7–0.8
Vanguard 75(B)	28(23.25)	43(46.5)	22(23.25)	1.30	0.5–0.7
Vanguard 75(C)	10(8.25)	14(16.5)	9(8.25)	0.82	0.5–0.7
Segregation within segregating families				*3:1*	
Vanguard 75(A)	660(667)	---	230(223)	0.08	0.7–0.8
Vanguard 75(B)	517(516)	---	171(172)	0.01	0.9–0.95
Vanguard 75(C)	148(150)	---	52(50)	0.11	0.7–0.8

gene notation as described by Robinson et al. (5).] M648-2 x 72-473 and its reciprocal both produced F_1 plants that were chlorophyll-deficient. The appearance of the F_1 and both parents was the same; therefore, the gene must be the same in each source. It is named *chlorophyll deficient-2* and symbolized *cd-2*.

A description of the phenotype when grown from seed follows. Cotyledons are light green with a yellowish cast. First true leaves are yellow-green with a green band along the midvein. At the 5- to 6-leaf stage, the leaves are blotchy yellow-green and green. Later, older leaves become markedly yellowed with green areas surrounding the veins. At this stage, the youngest leaves appear normal. As the plants grow older, the overall appearance of the plants becomes nearly normal.

Early flowering. In a pot containing seedlings of 56679, a crisphead type breeding line (developed by T.W. Whitaker from a cross between a butterhead, 'May King', and 50588, a crisphead breeding line of the 'Vanguard' type), one plant bolted and flowered while still in the pot. It produced a few flowers and few seeds per flower. I designated the off-type as 56679E (E = early) and made a cross with 'Salinas' as male parent. Four seeds were produced. Plants from 2 of these seeds bolted and flowered after a normal heading sequence. The other 2 plants bolted and flowered early. The former produced all normal (late) plants and the latter segregated late and early, showing that early flowering was dominant. (Flowering time is measured as the number of days from planting to first open flower on a plant.)

Two additional crosses (A and B) were made with 'Salinas' and 3 (A, B, and C) with 'Vanguard 75'. All F_1s were early, except from one cross between a late plant from the original mutant and 'Salinas' (B).

Five F_2 populations were grown. The population from the late F_1 did not segregate; all plants grew normally and bolted late, ranging from 105–156 days to first flower. The other F_2 populations segregated approximately 3 early : 1 late (Table 3). Early and late classes were easily separated in the 4 segregating populations, as there were gaps of 10, 23, 46, and 41 days, respectively, as listed in Table 3, between the last of the early and the first of the late flowering groups. Mean flowering times for the late classes were about double those of the early classes (Table 4). The range of flowering time for the early classes was about 45 days and for the late classes about 60 days. Fig. 1 illustrates the bimodal distribution of flowering times for one cross, 56679E x 'Vanguard 75' (A).

Therefore, a single gene controls flowering time and earliness is dominant. This is confirmed by among- and within-family F_3 segregation in the 3 'Vanguard 75' crosses (Table 5). The original mutant produced some late plants and must have been heterozygous for the flowering gene.

Dominance is incomplete. The mean number of days to flowering differs significantly between homozygous and heterozygous early F_2 groups, as identified in F_3, by about 12, 15, and 5 days, respectively, for the 3 populations of the 'Vanguard 75' crosses (Table 6). The gene is named *Early flowering* and symbolized *Ef*.

Pericarp color. A gene for involucre shape was identified and named *plump involucre* (*pl*) in an earlier study (7). The mutant (recessive) appeared in a plant of 'Jade'.

'Jade' has a black pericarp, but it was noted that the plump mutant had a brown pericarp. Crosses were made with 3 black parents, 71-318 (*endive-like leaf*), 6583 *fr* (*fringe*), and PI 190906. The F_1s of all 3 crosses had black seed, indicating that black is

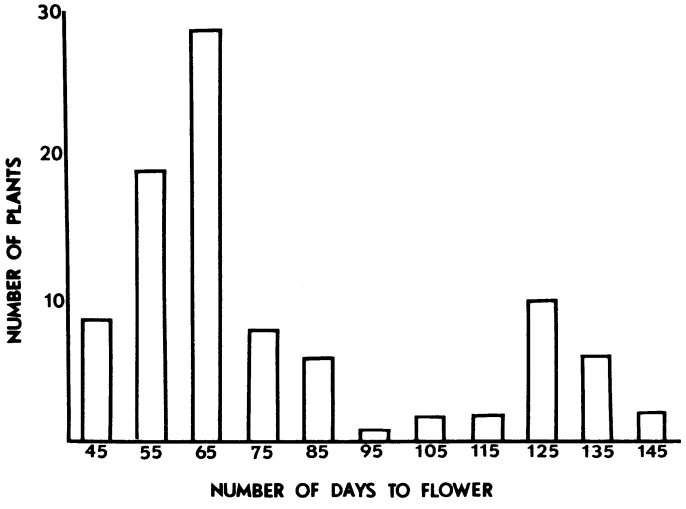

Fig. 1. Distribution of plants by flowering time classes in the F_2 generation of the cross 56679E x 'Vanguard 75' (A). Flowering times are midpoints of each 10-day class.

Table 6. Flowering time of F_2 plants classified as homozygous early or heterozygous early from F_3 data; Student's t test for nonpaired comparisons.

Population: 56679E x	Mean days to first flower: Homozygous early	Heterozygous early	t	P
Vanguard 75(A)	54.7	66.7	5.1	<0.01
Vanguard 75(B)	54.4	69.5	7.6	<0.01
Vanguard 75(C)	47.2	52.1	5.7	<0.01

Table 7. Inheritance of black vs. brown pericarp in F_2 populations of 3 crosses with Jade *pl*; expected numbers in parentheses.

Populations	Observed (expected) Black	Brown	χ^2 (3:1)	*P*
Jade *pl* x 6583 *fr*	494(520)	199(173)	5.21	0.02–0.05
71-318 x Jade *pl*	513(539)	206(180)	5.01	0.02–0.05
Jade *pl* x PI 190906	531(535)	182(178)	0.12	0.7–0.8
Total	1538(1593)	586(531)	7.60	<0.01
Heterogeneity (2 df)			2.36	0.3–0.5

dominant. The F_2 populations segregated for black and brown (Table 7).

A single gene hypothesis, with black dominant to brown, appeared most reasonable. However, 2 F_2 populations showed a significant excess of brown plants. The excess for all 3 together was highly significant (Table 7).

Jade *pl* also was crossed to 2 white parents 72-473 (*chlorophyll deficient-2*) and M400-27-23 (*virescent*). Earlier work showed that black vs. white pericarp color is a single-gene trait, with black dominant (*white*, *w*) (2). Both F_1s had black seed.

The F_2 populations segregated for black, brown, and white. The 72-473 x Jade *pl* population segregated 9 black : 3 brown : 4 white, as expected on a hypothesis of recessive epitasis involving 2 loci, both with dominance (Table 8). If white is excluded, segregation for black and brown was 3 : 1 (χ^2 = 1.18, P = 0.2–0.3). The M400-27-23 x Jade *pl* F_2 population showed a highly significant shortage of white plants (Table 8). The *white pericarp* gene *w* is closely linked to the leaf color gene *virescent* (*vi*) (6). Virescent plants are less viable than normal ones (7). There was a significant shortage of virescent plants, and as M400-27-23 has the genotype *w vi*/*w vi*, a deficiency of white plants would be expected.

F_3 families were grown from black F_2 plants of the 72-473 x Jade *pl* cross and from black and brown F_2 plants of the M400-27-23 x Jade *pl* cross. According to hypothesis, families from black F_2 plants should be all black; black and brown; black and white; and black, brown, and white in the ratio 1:2:2:4. Combining classes to calculate segregation of black and brown only, the families should appear in the ratio 1 all black : 2 black and brown. F_3 families from brown F_2 plants should segregate 1 all brown : 2 brown and white. Actual numbers of families were as expected according to the hypothesis (Table 9).

Within segregating families from black F_2 plants, the expectations are 9 black : 3 brown : 4 white in families segregating for all 3 colors and 3 black : 1 white in families segregating for those 2 colors. Segregation for black and brown, excluding white segregates, also should be 3:1. Within families from brown plants, segregation for brown and white also should be 3:1. Actual segregation within families was as expected (Table 10).

The cumulative evidence from F_2 and F_3 data supports the hypothesis for a 2nd locus for pericarp color. The 2 loci for pericarp color interact, giving a 9:3:4 ratio in F_2 (recessive epistasis). The gene for brown pericarp is not named here pending resolution of its relationship with *plump involucre* (*pl*), described below.

Table 8. Inheritance of black, brown, and white pericarp color in F_2 populations of 2 crosses with Jade *pl*; expected numbers in parentheses.

Populations	Observed (expected) Black	Brown	White	χ^2 (9:3:4)	*P*
72-473 x Jade *pl*	417(431)	154(143)	194(191)	1.35	0.5–0.7
M400-27-23 x Jade *pl*	424(415)	166(139)	149(185)	12.44	<0.01

Table 9. Inheritance of pericarp color in crosses with Jade *pl*; expected numbers in parentheses.

1. Segregating among F_3 families from black F_2 plants (72-473 x Jade *pl*)

Including white		*Excluding white*	
All black	5(4.4)	All black	13(13.5)
Segregating		Segregating	27(26.5)
Bl:br	7(8.9)	χ^2 (1:2)	0.06
Bl:wh	8(8.9)	*P*	0.8–0.9
Bl:br:wh	20(17.8)		
χ^2 (1:2:2:4)	0.85		
P	0.8–0.9		

2. Segregation among F_3 families from brown F_2 plants

	72-473 x Jade *pl*	*M400-27-23* x Jade *pl*
All brown	10(9)	9(10.7)
Segregating (*br:wh*)	17(18)	23(21.3)
χ^2 (1:2)	0.16	0.78
P	0.5–0.7	0.3–0.5

Results and Discussion

Linkage studies

Lettuce crosses are difficult to obtain without getting some selfed seed because of the flower structure. This makes backcross segregation unreliable and, therefore, all data are from F_2 populations and F_3 families.

Involucre shape and pericarp color. Brown pericarp and involucre shape (plump) segregated together in the crosses described above (Table 11). Linkage, in the coupling phase, was indicated. However, there were no recombinant plants in 2 of the 5 F_2 populations studied, and a total of only 12 in the remaining 3 populations. Also, F_3 progeny tests had disclosed occasional misreading of the involucre trait in the F_2. It was possible, therefore, that the 12 recombinants also were misread and that pleiotropy, rather than linkage, would account for the relationship between the 2 traits.

Progeny tests of the 12 F_2 plants were conducted. Nine plants had been classed as plump black and 3 as normal brown. Eight of the plump black plants produced progenies that were all normal or segregating for the involucre trait and all black or segregating for the color trait, indicating that the F_2 plants were

Table 10. Inheritance of pericarp color in Jade *pl* crosses.

Cross	Observed (expected) Black	Brown	White	χ^2	*P*
Within segregating F_3 families from black F_2 plants					
72-473 x Jade *pl*					
Including white					
Bl:wh (3:1)	54(53)	---	17(18)	0.08	0.7–0.8
Bl:br:wh (9:3:4)	128(122)	39(40)	49(54)	0.87	0.5–0.7
Excluding white (3:1)	186(178)	52(60)	---	1.43	0.2–0.3
Within segregating F_3 families from brown F_2 plants (3:1)					
72-473 x Jade *pl*	---	140(142)	49(47)	0.12	0.7–0.8
M400-27-23 x Jade *pl*	---	154(161)	61(54)	1.21	0.2–0.3

Table 11. Evidence for linkage between loci for pericarp color and involucre shape; expected ratio 9:3:3:1 (coupling phase).

F_2 populations	Observed (expected)				Linkage	
	Normal-black	Normal-brown	Plump-black	Plump-brown	χ^2	P
72-473 x Jade *pl*	412(321)	1(107)	5(107)	153(36)	617	<0.01
Jade *pl* x 6583 *fr*	390(274)	0(92)	0(92)	199(31)	843	<0.01
71-318 x Jade *pl*	512(404)	2(135)	1(135)	204(45)	834	<0.01
M400 x Jade *pl*	421(332)	0(110)	3(110)	165(37)	681	<0.01
Jade *pl* x PI 190906	531(391)	0(131)	0(131)	182(43)	743	<0.01
Total	2266(1790)	3(596)	9(596)	903(199)	3781	<0.01

actually normal black. The 9th plant produced all plump brown progeny, indicating that the F_2 plant was plump brown.

Two of the normal brown F_2 plants produced progeny that were normal or segregating for involucre shape and all brown for color. The F_2 plants, therefore, were classified correctly. The 3rd plant produced no progeny. The involucres of the F_3 plants, though classed as normal, were consistently shorter than those on normal black plants, averaging one cm in length compared to 1.3 cm for the typical normal type. However, the tips of the involucres on the normal brown plants were tapered in a concave fashion, and not blunt and straight as with the plump phenotype.

The traits are, therefore, either very closely linked or pleiotropic. If linked, the expected proportion of recombinants in the 5 populations together is on the order of 0.001 and the fact that no plump black recombinants appeared is not improbable. It also is possible that they had appeared and had been classified improperly as normal black or, less likely, as plump brown. If pleiotropy is the mechanism, then it is necessary to account for the 2 normal brown plants. It is possible that the shortened involucres were an unusual manifestation of the plump trait, and that they were actually plump brown.

Leaf type (endive) and pericarp color. A gene, *white* (*w*), controls pericarp color (2). The gene *endive-like* (*en*) controls leaf type (8). Five crosses were made with 71-318, a mutant line with the endive-type trait. 71-318 has black pericarp; the other parents were all white. The F_2 population of the cross 71-318 x M400-27-23 had too many parental types and too few recombinant types, indicating linkage. Two of the 4 remaining populations showed a nonsignificant bias in the same direction. For the total of 5 populations, linkage was indicated, at the 5% level of significance (Table 12).

The linkage value was estimated from the combined data as p = 0.468 ± 0.014. Heterogeneity χ^2, with 4 df, was 5.96, with P = 0.2–0.3, showing that the 5 sets of data were all reliable estimators of the recombination value. This might be expected, even though only one set actually indicated linkage, because the estimated value is so close to 0.50 (independent assortment). Data showing linkage of both genes to a 3rd gene will be conclusive evidence for linkage.

Chlorophyll deficiency (virescent) and leaf type (fringe). The virescent and fringe traits are each controlled by recessive alleles, *virescent* (*vi*) and *fringe* (*fr*) (6, 7). The cross 6583 *fr* (*fringe* x M400-27-23 (*virescent*) was made. The F_1 was normal for both traits. The F_2 segregated with too few recombinant (normal-normal and fringe-virescent) plants and too many of the parental types, which indicated linkage (Table 13). The recombination value was calculated as p = 0.251 ± 0.035.

Spininess and anthocyanin. The production of anthocyanin depends upon 2 complementary loci (*Cc* and g^+g). At least one dominant allele from each gene is required to produce red coloring in leaves and stems (g^+g was formerly designated *Tt*) (5, 9). PI 190906 has anthocyanin and spines. The cross Jade *pl* x PI 190906 segregated for both red color and spininess in F_2 (Table 14). Spininess was dominant. Segregation for spininess vs. spinelessness fits a 13:3 ratio (χ^2 = 0.07, P = 0.7–0.8) and gives a poor fit to a 3:1 ratio (χ^2 = 16.52, P < 0.01). However, spininess has been reported to be inherited as a single gene trait by Durst (2) and by Lindqvist (3). Durst reported on several crosses and several F_2 populations of each cross. Segregation in most populations was close to 3:1, but others had deviations giving both higher and lower ratios. Lindqvist's F_2 data may be interpreted equally well as fitting a 13:3 as a 3:1 ratio. In addition, there was a significant shortage of green plants (χ^2 = 6.29, P < 0.01). Therefore, linkage was calculated based on expectation of 9:3:3:1 and 39:9:13:3 ratios of red-spines, red-no spines, green-spines, and green-no spines and, because of the disturbed red-green segregation, with contingency tables based on marginal totals. All 3 calculations yielded significant χ^2s for linkage (Table 14).

Linkage value was estimated as p = 0.247 + 0.022 based upon 39:9:13:3 and as p = 0.193 ± 0.027 based upon 9:3:3:1.

Table 12. Evidence for linkage between genes for *endive-like* leaf and pericarp color; expected ratio 9:3:3:1 (repulsion phase).

F_2 population	Observed (expected)				Linkage	
	Normal-black	Normal-white	Endive-black	Endive-white	χ^2	P
71-318 x Calmar	214(213)	74(77)	68(65)	23(24)	0.30	0.5–0.7
71-318 x 71-461	257(264)	91(88)	96(88)	25(29)	1.66	0.1–0.2
71-318 x M400-27-23	177(184)	73(61)	64(61)	13(6)	4.69	0.02–0.05
71-318 x 9123	104(101)	35(23)	33(33)	6(11)	2.48	0.1–0.2
71-318 x 72-473	390(403)	144(134)	139(134)	43(45)	1.36	0.2–0.3
Total	1142(1166)	417(389)	400(389)	115(130)	4.54	0.02–0.05
Heterogeneity (4 df)					5.96	0.2–0.3

Table 13. Evidence for linkage between genes for *virescent* and *fringe*, repulsion phase.

F_2 population	Observed (expected[z])				Linkage χ^2	P
	Normal-normal	Normal-fringe	Virescent-normal	Virescent-fringe		
6583 *fr* x M400-27-23	323(361)	205(167)	150(112)	14(52)	53.31	<0.01

[z]Calculated from marginal totals because of disturbed ratio, normal : fringe segregation.

Further work is required to reconcile this difference. The genes linked are one member of the complementary pair for red color and a gene for spininess, possibly one of 2 if epistasis is involved. The red gene is identifiable as *Cc* from the evidence of other crosses involving Jade *pl*.

Other linkage detection tests. Linkage χ^2s and probabilities for several other combinations are shown in Table 15. Independent assortment was shown clearly between most pairs. However, the combinations of *pl* and *C*, *g*; *en* and *vi*; and *w* and *Dm-8* showed biases that indicated that they might be loosely linked pairs.

Lettuce linkage map. Two linkage groups have been reported previously. Lindqvist (3) reported a group of 4 genes. Ryder (8) reported a group of 3 genes. Two genes (*vi* and *en*) may be added to the latter group. The order previously reported was *w—fr—ms-6*. Gene *vi* is linked to *fr* and closely to *w* and therefore must be between them, as the sum of the map units is less than that between *fr* and *w*. The *en* gene is linked loosely to *w* and may be on either side. However, *en* and *vi* may be linked loosely and *en* and *fr* are not linked. Therefore *en* probably is to the left of the group as illustrated:

en——w—vi——fr——ms-6

Modified genetic relationships

Endive and fringe. The recessive traits *endive* and *fringe* each cause a severe distortion of the shape of the lettuce leaf (7, 8). The cross 71-318 (*en en*) x 6583 fr (*fr fr*) produces a normal F_1 phenotype. The F_2 consists of normal, *fringe*, and *endive* phenotypes. Some of the *endive* plants showed the trait in a more extreme condition: the leaves were narrower and more highly frilled than usual. I named these "*extreme endive*" and postulated that they were genetically double-recessive (*fr fr en en*). F_2 segregation was 308 normal, 113 *fringe*, 82 *endive*, and 33 *extreme endive*, with χ^2 (9:3:3:1) = 5.37, P = 0.1–0.2.

Thirty F_3 families from *endive* F_2 plants and 26 from *fringe* plants were grown. *Endive* F_2 plants should be, according to the hypothesis, *fr*$^+$ *fr*$^+$ *en en* and *fr*$^+$ *fr en en* and *extreme endive* should be *fr fr en en* and the 3 genotypes should be in the ratio 1:2:1. All families bred true for *endive*. Eleven of these, somewhat more than ¼, were of the extreme type as expected. *Fringe* F_2 plants should be *fr fr en*$^+$ *en*$^+$ or *fr fr en*$^+$ *en* in a ratio of 1:2, according to the hypothesis. One-third of the families were all *fringe* and ⅔ segregated *fringe* and *endive*, as expected.

Additional evidence was obtained by crossing: 1) *fr*$^+$ *fr*$^+$ *en en* (*endive*), 2) *fr*$^+$ *fr en en* (*endive*), and 3) *fr fr en en* (*extreme endive*) by *fr fr en*$^+$ *en*$^+$ (*fringe*). These crosses should produce:

1) all normal + *endive* selfs
2) ½ normal + ½ *fringe* + *endive* selfs + *extreme endive* selfs
3) all *fringe* + *extreme endive* selfs

The combined progenies of crosses 1 and 2 should produce normal and *fringe* plants in the ratio 2:1, plus endive and *extreme endive* selfs. The actual numbers were: 1 normal, 9 *fringe*, 7 *endive*, and 3 *extreme endive*. The ratio of normal : *fringe* did not meet expectation. This could be due to a misreading of phenotype or to the small size of the sample.

The progeny of cross 3 included 7 *fringe* plants, plus 4 *extreme endive* selfs, as expected. It seems reasonable, therefore, to accept the hypothesis that *fr fr en en* produces an *extreme endive* phenotype.

Virescent and golden. These are both recessive, chlorophyll-deficient forms. The cross 9123 x M400-27-23 (*golden* x *virescent*) produced 3 phenotypes: *normal green* (266), *virescent* (91) and *golden* (116), in the F_2. This gives a close fit to the epistatic ratio 9:3:4 (χ^2 = 0.07, P = 0.95–0.98), expected if it is hypothesized that *go go vi vi* is *golden*.

The F_2 genotypes 1) *go go vi*$^+$ *vi*$^+$, 2) *go go vi*$^+$ *vi*, and 3) *go go vi vi* would all be *golden* and would breed true. If crossed by *go*$^+$ *go*$^+$ *vi vi* (*virescent*) as the male, they would produce, respectively:

1) all normal + *golden* selfs
2) ½ normal, ½ *virescent* + *golden* selfs
3) all *virescent* + *golden* selfs

These would be in the ratio of 1:2:1. Ignoring the selfs, a 3:1 ratio of normal + segregating families to *virescent* families would be expected. (Some families were difficult to classify as normal or segregating and the 2 groups were counted together.) The actual ratio was 31:12 (χ^2 = 0.18, P = 0.8–0.9), confirming the hypothesis.

Golden and chlorophyll deficient-2. The cross 9123 x 72-473 (*golden* x *chlorophyll deficient-2*) produced 3 phenotypes in the F_2: normal (363), *chlorophyll deficient* (131), and *golden* (143).

Table 14. Evidence for linkage between genes for red color and spininess in cross Jade *pl* x PI 190906.

F_2 segregation	Red-spines	Red-no spines	Green-spines	Green-no spines	Linkage χ^2	P
Observed	512	52	70	79		
Expected (9:3:3:1)	401	134	134	44	132.9	<0.01
Expected (39:9:13:3)	435	100	145	33	133.2	<0.01
Contingency table	460	104	122	27	154.2	<0.01

Table 15. Linkage detection tests showing no evidence for linkage. Expected ratios of F_2 phenotypes (1 = *A-B-* type; 2 = *A-bb* type; 3 = *aaB-* type; 4 = *aabb* type).[z]

Loci compared[y]	Obs. no. in each phenotype 1	2	3	4	Total	Linkage χ^2	*P*
cd-2;c,g[x]	263	81	100	33	478	0.30	0.5–0.7
cd-2;fr	198	72	67	30	367	0.81	0.3–0.5
cd-2;mo	254	90	102	32	478	0.18	0.5–0.7
cd-2;ms-6	457	209	154	80	900	0.64[w]	0.3–0.5
cd-2;pl	421	162	134	48	765	0.18	0.5–0.7
cd-2;sc	321	96	119	34	570	0.03	0.8–0.9
cd-2;w[u]	1013	331	349	120	1813	0.15	0.5–0.7
en;cd-2	395	139	138	44	716	0.55	0.3–0.5
en;c,g[x, v]	323[r]	272	114	94	803	0.35	0.5–0.7
en;fr	308	113	82	33	536	0.35	0.5–0.7
en;lg[u]	260	78	96	40	474	2.13	0.1–0.2
en;mo	144[q]	57	289	108	598	0.08	0.7–0.8
en;vi[t]	183	69	63	14	327	2.72	0.05–0.1
go;u	286	91	100	27	504	0.41	0.5–0.7
go;vi	266[s]	91	---	---	357	0.05	0.8–0.9
pa;en	115	45	52	22	234	0.10	0.7–0.8
pa;go	273	99	103	28	503	1.47	0.2–0.3
pa;mo	348	114	138	46	646	0.00	>0.99
pl;c,g[x]	412	119	152	30	713	2.85[w]	0.05–0.1
u;mo	372	123	114	37	646	0.01	0.98–0.99
vi;pl	423	162	103	51	739	1.94[w]	0.1–0.2
w;Dm-8	239	63	55	24	381	3.26[w]	0.05–0.1

[z]Comparisons based upon 9:3:3:1 F_2 ratios, except as noted.
[y]Gene symbols: *pa* = pale yellow flower; *go* = golden flower; *en* = endive-like leaf; *c,g* = complementary loci; alleles for no anthocyanin; *vi* = virescent; *mo* = mosaic resistance; *fr* = fringe leaf; *lg* = light green; *cd-2* = chlorophyll deficient; *u* = unlobed leaf; *pl* = plump involucre; *Dm-8* = downy mildew resistance; *w* = white pericarp; *sc* = frilled leaf margin; *ms-6* = male sterile; *br* = brown pericarp.
[x]One or both anthocyanin genes were segregating and were not identifiable.
[w]Calculated from 2 × 2 contingency tables using marginal totals because of disturbed ratios for one or both genes.
[v]Three populations combined.
[u]Two populations combined.
[t]Classified F_2 (1:2:1/3:1).
[s]3:1 within nongolden class.
[r]Expected ratio 27:21:9:7.
[q]Expected ratio 3:1:6:2.

Two alternative hypotheses may be stated: 1) The *golden* phenotype included *go go cd-2 cd-2*, giving an expected 9:3:4 ratio (χ^2 = 2.69, *P* = 0.2–0.3); and 2) The genotype *go go cd-2 cd-2* is lethal, giving an expected 9:3:3 ratio (χ^2 = 3.17, *P* = 0.2–0.3).

The *golden* genotypes under the first hypothesis would be *go go cd-2*$^+$ *cd-2*$^+$, *go go cd-2*$^+$ *cd-2*, and *go go cd-2 cd-2*, in the ratio 1:2:1. When crossed by *go*$^+$ *go*$^+$ *cd-2 cd-2*, we would expect, ignoring *golden* selfs, 1 normal : 2 segregating : 1 *chlorophyll deficient* families.

Under the 2nd hypothesis, the *golden* genotypes would be *go go cd-2*$^+$ *cd-2*$^+$ and *go go cd-2*$^+$ *cd-2* (ratio 1:2). the same cross by *go*$^+$ *go*$^+$ *cd-2 cd-2* would produce no *chlorophyll deficient* families. The actual ratio was: 21 normal : 19 segregating : 7 *chlorophyll deficient*.

Seven of the families rated as normal had 4 plants or fewer. Some or all may have been segregating. The ratio of normal to segregating therefore was probably close to 1:2. There were 7 *chlorophyll deficient* families; therefore, the *go go cd-2 cd-2* genotype existed. As there were 2 to 3 times as many normal as deficient families, it is possible that *go go cd-2 cd-2* was partially lethal.

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