kills them, these trees will live indefinitely and their exotic appearance will continue to taint the native forest. They could easily be killed and then the native vegetation would rapidly replace them.

Sapodilla (*Manilkara zapota*), Key lime (*Citrus aurantifolia*), and tamarind (*Tamarindus indica*) are common throughout the Keys since they have been planted around many old homesites. They blend in well with the native vegetation and are almost considered to be a part of it now. Although these species are thriving on Lignumvitae they do not aggressively spread into the hammock.

The experience with plant introduction in Lignumvitae Key indicates that the principal danger from introduced plants escaping is in areas disturbed by man. Care should be exercised when new plants are brought in to make sure that they are not weed species where they occur naturally. Special consideration should be given to plants that are normally spread by birds to make sure that they will not endanger a new environment.

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PHYSIOLOGICAL DISORDERS OF LEAVES OF CHRYSANTHEMUM CULTIVARS RELATIVE TO ACCUMULATION OF EXCESS CARBOHYDRATE

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Abstract

Nineteen chrysanthemum cultivars, including both pompon and standard types, were grown in a saran cloth house in the spring season to observe differential foliar reactions associated with the accumulation of excess photosynthate (carbohydrate) or the "excess photosynthate syndrome" (EPS). The overall condition including bronzing, leaf roll, necrosis, thickening, and yellowing are collectively described as EPS. Standard cultivars exhibited a greater degree of development of EPS than did pompons. Total indexes of EPS were statistically correlated with glucose, sucrose, total sugars, and total carbohydrates in leaves, significant at the 1% level. Starch content of leaves was significantly correlated at the 5% level while the correlation coefficient for fructose was not significant. Cut flower stems, held in sucrose (0, 2, 4 and 8%) solutions containing 200 ppm 8-hydroxyquinoline citrate for the development of EPS, provided direct evidence of a cause-effect relationship. Increasing levels of sucrose caused increasing yellowing, thickening of leaves, and increasing anthocyanin content. Leaf roll and dry weight of leaf tissue increased with increasing sucrose. Chlorophyll content decreased with increasing sucrose. Stems held in 0% sucrose did not develop EPS symptoms while those held in 2, 4 and 8% developed most of the symptoms in proportion to sucrose level.

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Introduction

Foliage of the chrysanthemum and tomato plants frequently exhibits (4, 5) a disorder that cannot be associated with any pathogen. Although the symptom development may be related to nutrition, culture and climate, the prime causal factor appears to be the accumulation of excess photosynthate (carbohydrates) and will be referred to as the "excess photosynthate syndrome" (EPS). The linkage of these disorders with excess carbohydrates is based on several lines of evidence (4, 5) but cannot be regarded as an established fact. The progression of symptom development associated with high light intensity has been described previously (4). The chlorotic pattern on lower leaves may easily be mistaken for magnesium deficiency. Sucrose in flower preservatives has been associated (3) with the development of chlorosis of the leaves of chrysanthemum cut-flowers.

The salability of chrysanthemum cut flowers occasionally may be adversely affected by the physiological disorder depending on variety, climate and culture. The objective of this study was (a) to determine the degree of susceptibility of 19 cultivars to the disorder and (b) to determine the correlation of various carbohydrates in leaves with severity of EPS.

Materials and Methods

Rooted cuttings were planted in triplicate randomized block ground bed plots in a saran cloth house (approximately 25% shade) February 4. Thirty plants, 6 across and 5 the length of the bed, constituted the experimental unit. Soil had been previously amended with 1 bale of peat per 72 x 3 foot bed and superphosphate and 6-6-6 fertilizer both containing trace elements at 500 lb per A each. Liquid fertilizer (NH_4NO_3 plus KNO_3) was applied weekly at 30 lbs each N and K_2O per A. Plants were lighted until March 5 and were pinched February 25. Standard cultivars were pruned to 2 stems per plant. Pompon cultivars were pruned to 3 stems per plant. Varieties are listed in Table 1.

Insecticide sprays were applied as required but no fungicides were used so that disease susceptibility could be observed. Records of symptoms of the physiological disorder were made on disease-free leaves on the lower half of the plant, and similar leaves were sampled for carbohydrate analyses. Ratings were made on leaf condition May 12 and leaves were sampled May 14. Carbohydrates were determined by previously described (4) methods.

Triplicate stems of 'Iceberg' and 'Puritan' which had initiated flower buds (2-5 mm diameter) were placed in holding solutions containing 200 ppm 8-hydroxyquinoline citrate and 0, 2, 4 and 8% sucrose, based on results obtained by Marousky (2). Stems were held in the laboratory at 75F ± 2, lighted continuously with cool white fluorescent tubes at 225 ft-c. At the end of one week, foliar chlorophyll content was determined by the method of Arnon (1) and a visual rating was made for yellowing and anthocyanin development on a scale of 0 = none to 5 = maximum development.

Leaf disks were sampled for dry weight determination to show degree of growth and increased leaf thickness in response to sucrose as it would

Table 1. Carbohydrate contents, percent of fresh weight, of lower leaves of 19 chrysanthemum cultivars.

Cultivars	Fructose	Glucose	Sucrose	Total Sugars	Starch	Total Carbohydrates
Standards						
Albatross	0.13	0.42	0.14	0.69	0.30	0.99
Explorer	0.12	0.36	0.15	0.63	0.22	0.85
Indianapolis Yellow	0.13	0.57	0.21	0.91	0.40	1.31
Mrs. Roy	0.14	0.51	0.20	0.85	0.54	1.39
Southern Comfort	0.13	0.41	0.16	0.70	0.23	0.93
Pompons						
Beauregard	0.10	0.37	0.17	0.64	0.19	0.83
Belair	0.09	0.39	0.15	0.63	0.26	0.89
Bluechip	0.05	0.30	0.16	0.51	0.26	0.77
Dolly	0.09	0.43	0.16	0.68	0.36	1.04
Flamenco	0.07	0.31	0.13	0.51	0.12	0.63
Iceberg	0.10	0.32	0.12	0.54	0.16	0.70
Iceland	0.06	0.32	0.12	0.50	0.24	0.74
Manatee Iceberg	0.09	0.36	0.15	0.60	0.16	0.76
Pink Marble	0.12	0.34	0.13	0.59	0.28	0.87
Show Off	0.12	0.49	0.17	0.78	0.36	1.14
Starburst	0.08	0.29	0.11	0.48	0.13	0.61
Yellow Iceberg	0.09	0.36	0.11	0.56	0.15	0.71
Yellow Knight	0.14	0.46	0.16	0.76	0.57	1.33
Yellow Shasta	0.10	0.37	0.19	0.66	0.75	1.41
Mean	0.10	0.39	0.15	0.64	0.30	0.94

Table 2. Mean rating indexes* for visible leaf abnormalities in relation to foliar carbohydrates.

Cultivar	Bronzing	Leaf Roll	Necrosis	Thickening	Yellowing	Total of Rating Indexes
Standards						
Albatross	0.2	2.7	1.5	2.8	1.8	9.0
Explorer	0.0	2.3	4.7	2.5	2.0	11.5
Indianapolis Yellow	0.0	3.0	1.7	4.2	3.0	11.9
Mrs. Roy	1.5	2.8	1.3	3.8	1.7	11.1
Southern Comfort	0.0	3.5	1.3	3.5	1.8	10.1
Pompons						
Beauregard	0.1	2.3	1.4	3.0	2.0	8.8
Belair	0.2	0.7	0.6	0.8	0.3	2.6
Bluechip	0.0	3.2	1.7	2.8	1.7	9.4
Dolly	1.2	3.5	1.8	2.8	3.0	12.3
Flamenco	0.2	2.2	1.7	2.5	2.3	8.9
Iceberg	0.3	0.4	0.5	0.2	0.1	1.5
Iceland	0.0	0.0	0.7	0.7	1.0	2.4
Manatee Iceberg	0.0	0.3	0.4	0.5	0.7	1.9
Pink Marble	0.5	0.2	0.3	1.0	0.5	2.5
Show Off	0.2	3.2	3.2	3.2	4.2	14.0
Starburst	0.0	0.0	0.3	0.0	0.2	0.5
Yellow Iceberg	0.2	0.4	0.3	0.4	0.5	1.8
Yellow Knight	1.2	1.7	1.2	1.5	2.0	7.6
Yellow Shasta	1.7	3.7	1.3	2.8	2.7	12.2
Mean	0.4	1.9	1.4	2.0	1.7	7.4

*0 = no abnormality of the respective categories, 1 to 5 = increasing degree of abnormality.

pertain to EPS. Disks were removed from the middle of the leaf to include the mid-rib. Leaves sampled were midway up the 16 inch stems.

Results

The results of sugars and starch determinations are presented in Table 1. Of the sugars determined, fructose was present in lowest amounts followed by sucrose and glucose. Starch accounted for slightly less than one-third the total carbohydrate contents. The 19 cultivars show a wide variability in carbohydrate contents. The standard cultivars contained an average of 24% more total carbohydrates in the leaves than the pompons.

The results of visual ratings of middle to lower leaves are given in Table 2. Bronzing was present at a low level while the other categories associated with accumulation of carbohydrates received higher mean rating indexes. The standard cultivars had consistently high rating totals while pompon cultivars were quite variable in terms of the totals of rating indexes. The standard cultivars received an average of 73% greater total indexes of EPS than did the pompons.

Cultivars are arrayed in Table 3 in the order of increasing relative indexes of the excess photosynthate syndrome to permit inspection of the systematically arranged data. Relative contents of three sugars, total sugars, starch and total carbohydrates are also listed. Correlation coefficients are presented (Table 3) for the relationship of index total to various categories of carbohydrate contents. Fructose contents were not significantly correlated with indexes while all other categories of carbohydrate contents were directly and significantly correlated with visual rating index tables. Sucrose had the highest degree of correlation followed by total carbohydrates, total sugars, glucose and starch in decreasing degree of positive correlation.

The data in Table 4 are presented relative to the hypothesis that foliar discoloration and thickening as part of the excess photosynthate syndrome

Table 3. Correlation of Indexes[a] of foliar symptoms indicative of the Excess Photosynthate Syndrome with relative carbohydrate contents of leaves.

Cultivar	Totals[b] of Mean Indexes	Fructose	Glucose	Sucrose	Total Sugars	Starch	Total Carbohydrates
Starburst	4	59	50	50	52	22	42
Iceberg	11	69	57	55	58	28	49
Manatee Iceberg	13	64	63	69	65	29	54
Yellow Iceberg	14	70	63	53	62	26	51
Iceland	17	46	56	58	55	43	53
Pink Marble	18	84	59	62	64	49	61
Belair	19	69	68	69	69	45	63
Yellow Knight	55	100	80	76	83	100	94
Beauregard	64	69	65	81	70	34	59
Albatross	65	98	73	68	76	53	70
Flamenco	65	52	54	62	56	22	45
Bluechip	67	40	52	77	56	45	55
Southern Comfort	73	92	71	75	75	41	65
Mrs. Roy	81	99	90	96	93	96	99
Explorer	83	84	63	73	69	38	60
Indianapolis Yellow	86	97	100	100	100	70	93
Yellow Shasta	88	71	65	89	72	88	100
Dolly	89	62	74	75	73	63	73
Show Off	100	85	86	82	85	64	81
Correlation coefficients		+0.34(ns)	+0.59[d]	+0.79[d]	+0.64[d]	+0.56[c]	+0.65[d]

[a]Relative values with maximum taken as 100, arrayed in order of increasing magnitude
[b]Totals of means of 0-5 ratings for increasing severity, or bronzing, leaf roll, necrosis, thickening and yellowing.
[c]Significant at the .05 level.
[d]Significant at the .01 level.

are related to carbohydrate levels. The data presented were obtained from 'Iceberg' and 'Puritan' cultivars. Chlorophyll content decreased with increasing sucrose resulting in visible effects as shown by the yellowing index. Anthocyanin development was not visibly apparent in the absence of sucrose but increased as the sucrose content of the holding solution was increased. With 'Iceberg', anthocyanin formed mainly in the leaves while in the case of 'Puritan' anthocyanin was found in the stems. The thickening index was based on palpable thickness as well as an associated "brittleness" of leaves which could be evaluated separately but appears to be a result of the thickening process.

Table 4. Effect of sucrose concentration in holding solutions[a] on development of symptoms of the Excess Photosynthate Syndrome.

Percent sucrose in holding solution	Chlorophyll content, mg/100 mg fresh weight			Mean yellowing index[d]			Mean anthocyanin[e] index			Mean thickening index[d]			Dry weight of leaf disks mg/cm			Leaf roll index[d]			Mean leaf area cm^2 of fifth leaf down stem
	I[b]	P[c]	Mean	I	P	Mean	I	P	Mean	I	P	Mean	I	P	Mean	I	P	Mean	P
0	0.15	0.14	0.14	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.2	6.2	6.7	0.0	0.5	0.3	24
2	0.12	0.12	0.12	1.2	.7	0.9	0.0	1.2	0.6	0.3	0.9	0.6	14.0	12.0	13.0	0.4	1.2	0.8	27
4	0.10	0.10	0.10	2.2	1.7	1.9	1.5	2.7	2.1	1.2	2.2	1.7	17.3	15.3	16.3	1.4	2.3	1.9	32
8	0.07	0.09	0.08	4.5	2.7	3.6	4.0	4.0	4.0	1.7	3.0	2.4	21.1	19.8	20.5	1.7	2.7	2.2	31
LSD, .05 level			.02	0.7	0.7	0.5			0.6	0.4	0.4	0.3			1.5			0.5	

[a]All solutions contained 200 ppm 8-hydroxyquinoline citrate.
[b]Iceberg cultivar.
[c]Puritan cultivar.
[d]Visual rating index, 0 to 5 increasing degree of visible effect.
[e]Anthocyanin in Iceberg primarily in foliage; in Puritan anthocyanin only visible in stems.

The thickening indexes rated according to visible effects and leaf texture are strongly supported by the data in Table 4 on weights of leaf disks which given an alternative, quantitative measure.

Discussion

The fact that standard cultivars contained an average of 24% more total carbohydrates and received an average of 73% greater EPS rating indexes totals is probably related to the cultural practices of pruning to fewer stems and disbudding standard cultivars thereby forcing the photosynthate into less vegetative and flowering plant tissue. Experience with tomato EPS is that removal of vegetative growth, flowers and fruit, or in other words, the removal of the photosynthate "sink" that normally receives the carbohydrate, results in thickening, yellowing and rolling of leaves (4). In addition to this consideration, there may be a greater photosynthetic capacity in those cultivars which can produce large, standard blossoms. This capacity could then contribute to EPS.

The five categories of symptom expression in EPS (Table 2) appear from the data presented as well as a previous report (5) to be clearly related to the syndrome. Care must be taken, however, not to mistake symptoms of other physiological or genetic disorders that are similar in appearance. This question can frequently be resolved by examination of plants growing in outdoor beds. Those plants that receive most sunlight will display EPS if the cultivar is susceptible while plants receiving less sunlight should not. This would, of course, be only one line of evidence.

Inspection of the categories of data in Table 2 suggests that thickening of leaves is probably the best single index of the occurrence of EPS although the other symptoms are parts of the syndrome that collectively determine the degree of effect of EPS on salability of the cut-flowers. Examples of extremely adverse effects of EPS are not widespread. The standard 'Peter Johns' probably represents the best illustration of the potentially adverse effects of poor foliage caused by EPS.

Direct evidence is given in Table 4 that carbohydrates cause certain symptoms of EPS. Cut stems exhibit foliar defects due to excess sugar, namely, yellowing, anthocyanin development (as in bronzing), and an abnormally high degree of thickening as shown by visual rating indexes and the increasing dry weight of leaf disks related to increasing sucrose. The increased weight per unit area is probably due in part to increased carbohydrate, however, there appears to be a considerable degree of growth of leaf tissue, especially in the thickness of the veins and apparent expansion of leaves.

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