THE CLIMATIC DISTRIBUTION OF CERTAIN TYPES OF ANGIOSPERM LEAVES[1]

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The instability of the gross or superficial characters of leaves has been emphasized by many taxonomists, and by a number of morphologists who have desired to bring into the limelight the conservatism of internal structures. Indeed, the prevailing opinion among botanists seems to be that foliar characters, except among small groups of closely related species, are so unreliable as to be of little value in the study of relationship and phylogeny. The warmest supporters of the opposite view, as might naturally be expected, are to be found among those paleontologists whose attention has been focused upon the identification of leaf impressions.

It occurred to the writers that a careful study of the distribution of various types of Angiosperm leaves in the principal phytogeographical regions of the earth might throw some light upon the question of the conservatism of foliar characters and their modification by environmental factors.

Fortunately, the task of tracing the distribution of foliar structures, particularly of the more conspicuous external ones, is facilitated by the fact that there are now available numerous published floras and large herbaria where descriptions of the leaves of plants from various parts of the world can be obtained. It is to be regretted, however, that so many taxonomists have made their floras and collections representative of political rather than of phytogeographical areas, and that ecological notes usually are meager or entirely absent.

In the following pages are summarized the results of an investigation upon the leaf form of Dicotyledons, undertaken in an endeavor to secure more specific information in regard to the distribution of leaves and leaflets with entire and non-entire (*Crenulate*, *crenate*, *serrulate*, *serrate*, *denticulate*, *dentate*, *lobed*, *incised*, etc.) margins.

[1] Investigations upon the phylogeny of the Angiosperms, No. 6.

Table I[2] presents an analysis of the Dicotyledonous floras of various regions of the frigid, temperate, and tropical zones. The first column of figures on the left gives the total number of Dicotyledons, exclusive of aquatic, parasitic, and leafless forms, in the flora of each region. The three succeeding columns record the percentages of trees, shrubs (all ligneous forms except arborescent species) and herbs that occur in these floras; and in the last three columns are tabulated the percentages of the trees, of the shrubs, and of the herbs that have leaves or leaflets with entire margins.

TABLE I—*Group 1*

	Total Species	% *Trees*	% *Shrubs*	% *Herbs*	% Entire Trees	% Entire Shrubs	% Entire Herbs
Ellesmereland	68	0	9	91		100	48
N. E. Siberia	117	0	14	86		65	52

[2] Based upon analyses of the following floras:

North America: The Vascular Plants in the Flora of Ellesmereland, Simmons; An Illustrated Flora of the Northern United States, Canada, and the British Possessions, Britton and Brown; New Manual of Botany of the Central Rocky Mountains, Coulter and Nelson; Flora of Los Angeles and Vicinity, Abrams; Flora of the Southeastern United States, Small; Flora of the Florida Keys, Small; Flora Nicaragüense, Goyena; Flora of the British West Indian Islands, Grisebach.

South America: Flora Braziliensis, Martius and others; Historia Fisica y Politica de Chili, Botanica, Gay; Reports of the Princeton University Expeditions to Patagonia, 1896–1899, Botany, Macloskie.

Europe: English Botany, Sowerby and others; Flora des Nordostdeutschen Flachlandes, Ascherson and Graebner; Flora Rossica, Ledebour; Flora Analitica D'Italia, Fiori and Paoletti; Herbier de la Flore Française, Cusin and Ausberque; Compendio de la Flora Española, Lazaro e Ibiza.

Asia: Flora Rossica, Ledebour; Flora Orientalis, Boissier; Flora Simlensis, Collett; Flora of the Upper Gangetic Plain and of the adjacent Siwalik and Sub-Himalayan Tracts, Duthie; Flora of the Presidency of Bombay, Cooke; A Handbook of the Flora of Ceylon, Trimen; Materials for a Flora of the Malayan Peninsula, King and Gamble; Flora Indiae Batavae, Miquel; Flora Hongkongensis, Bentham; Flora of Manila, Merrill; Woody Dicotyledonous flora of east central China, herbarium of the Arnold Arboretum.

Africa: Manual of the Flora of Egypt, Muschler; Flora of Tropical Africa, Oliver, Thiselton-Dyer and others; Flora Capensis, Harvey and others; Flora of Mauritius and the Seychelles, Baker.

Australasia: Flora Australiensis, Bentham; Manual of the New Zealand Flora, Cheeseman.

Oceana: Flora of the Hawaiian Islands, Hillebrand.

Table I—*Group 2 and Group 3*

	Total Species	% *Trees*	% *Shrubs*	% *Herbs*	% Entire Trees	% Entire Shrubs	% Entire Herbs
E. C. North America	1,504	7	14	79	10	37	42
Rocky Mountains	1,413	1	10	89	0	40	52
N. Russia	356	2	14	84	0	35	42
C. Russia	1,225	3	10	87	0	36	42
S. Russia	2,319	4	9	87	8	52	44
England	1,273	2	11	87	3	37	35
N. E. Germany	1,166	2	12	86	0	29	45
France	3,924	2	9	89	4	53	48
S. E. Siberia	458	2	10	88	0	45	44
W. Siberia	1,085	3	10	87	0	57	45
Kamtschatka	301	1	17	82	0	35	33
	15,024				2	41	43
S. E. United States	4,451	6	18	76	36	54	48
Los Angeles	831	3	16	81	18	58	45
Chili	2,409	4	30	66	46	55	46
Patagonia	1,488	2	28	70	28	57	47
Spain	4,103	1	18	81	13	59	48
Italy	3,069	2	10	88	18	56	40
E. C. China	2,015				38	52	
S. New Zealand	713	8	33	59	53	68	43
Simla (mts.)	989	13	25	62	53	60	38
	20,068				34	58	44

Among woody plants, leaves and leaflets with entire margins are overwhelmingly predominant in tropical and subtropical environments. This is very nearly as pronounced among shrubs as it is among trees. In cold-temperate regions, on the other hand, trees with entire leaves and leaflets are extremely infrequent, and the leaf-margins of shrubs are on the average more than half non-entire. Warm-temperate regions are intermediate between tropical and cold-temperate ones, and the shrubs of frigid habitats resemble those of the tropics in having very high percentages of entire margins.

Among herbaceous plants, higher percentages of leaves and leaflets with entire margins occur in tropical and subtropical regions, but the contrast between the frigid, temperate, and tropical zones is less well marked than among trees and shrubs.

The somewhat paradoxical behavior of the leaves and leaflets of arborescent, as compared with herbaceous Dicotyledons, raises the question as to whether the entire and non-entire types of leaf-margins are determined by environmental influences, or whether they are

TABLE I—*Group 4*

	Total Species	% *Trees*	% *Shrubs*	% *Herbs*	% Entire Trees	% Entire Shrubs	% Entire Herbs
Florida Keys	473	8	37	55	84	83	64
Nicaragua	1,509	17	39	44	86	71	48
West Indies	2,209	19	52	29	88	71	61
Brazil	10,468	21	62	17	87	76	56
Hongkong	699	16	43	41	73	71	58
Flora Orientalis	9,771	4	13	83	71	72	53
Upper Gangetic Plain	1,084	15	31	54	73	71	45
Malay States	3,252	41	42	17	90	82	64
Ceylon	1,752	20	44	36	84	78	54
Manila	333	30	38	32	83	80	67
East Indies	6,389	30	45	25	81	75	49
Hawaii	521	26	50	24	78	61	45
Queensland	1,734	22	45	33	81	82	63
W. Australia	2,543	2	73	25	73	83	71
New South Wales	1,780	13	54	33	75	84	54
Victoria	1,152	6	50	44	87	84	52
Tasmania	662	4	48	48	82	77	45
Egypt	1,239	2	16	82	73	78	49
C. E. Africa	2,837	6	36	58	75	74	54
C. W. Africa	2,656	17	46	37	85	80	56
S. W. Africa	2,400	11	43	46	84	82	62
S. E. Africa	2,653	8	42	50	80	78	56
Southern Africa	7,783	2	55	43	73	74	53
Mauritius-Seychelles	545	17	49	34	88	84	65
	66,444				81	77	56

form-variations of little functional significance that are held on by heredity?

In the first place, the possibility suggests itself that the entire-leaved plants in temperate regions and the non-entire-leaved forms in tropical regions may occur in somewhat different environments from those occupied by the prevailing types of arborescent vegetation. A detailed examination of the regions and percentages given in Table I affords some evidence that seems to point in this direction. All the regions recorded are heterogeneous in that they contain in most cases more than one of even the principal plant formations. In group 2, those regions, Rocky Mountains, south Russia, France, Siberia, etc., which have larger areas of arid or physiologically dry environments, have higher percentages of entire-leaved shrubs. On the other hand, those regions of the tropics that have more extensive equable environments or moist cool uplands have higher percentages of herbs with non-entire leaves and leaflets.

The influence of uplands, in increasing the number of non-entire types in tropical and subtropical regions, is also shown in the following table. It is in marked contrast to the effects of high alpine or cold, dry, upland environments in temperate regions.

TABLE II—*Tropical or Sub-tropical*

	Lowlands (% Entire)			Uplands (% Entire)		
	Trees, Percent	Shrubs, Percent	Herbs, Percent	Trees, Percent	Shrubs, Percent	Herbs, Percent
Hawaii	84	71	67	70	50	24
Ceylon	88	81	61	72	75	34
Temperate						
S. New Zealand	53	64	37	100	76	50

In view of these facts, it is desirable to compare a lowland-tropical flora and a uniformly mesophytic cold-temperate one. The next table gives an analysis of two such floras. The mesophytic cold-temperate flora was reconstructed from that of east central North America (east of the 95th meridian and between the 40th and 50th parallels of latitude) by eliminating all extremely microphyllous forms, xerophytes, and plants growing in dry habitats. The lowland-tropical flora was made from that of Brazil, by including the plants of the lowlands of the Amazon valley and excluding those from the uplands of the southern, central, and eastern provinces.

TABLE III

	Entire %		
	Trees, percent.	Shrubs, percent.	Herbs, percent.
Mesophytic Cold-temperate (E. C. N. A.)	10	14	23
Lowland-tropical. (Brazil)	90	87	62

Of course, it should be kept in mind that prevailing climatic influences are not absolutely constant throughout these extensive areas. Furthermore, it is hardly to be expected that in any such arbitrarily selected region of North America there should be an abrupt transition from cold-temperate to warm-temperate or to arctic conditions.

It is significant, therefore, that those arborescent species which constitute the 10 per cent of entire-leaved plants in the mesophytic cold-temperate flora are all southern, warm-temperate types, most of which are at one extremity of their range, north of their region of optimum development. They are:

Quercus phellos L.	*Magnolia acuminata* L.
Q. imbricaria Michx.	*M. virginiana* L.
Cercis canadensis L.	*Gymnocladus dioica* (L.) Koch.
Nyssa sylvatica Marsh.	*Diospyros virginiana* L.

Among the entire-leaved shrubs and herbs there are many frigid and warm-temperate types that are largely confined to the northern or southern portions of the region respectively.

In considering the percentages of non-entire leaves in the lowland-tropical flora, it is important to note that the serrations, dentations, etc., of the non-entire leaves, particularly of trees and shrubs, are very frequently vestigial or rudimentary. In fact, not only are the non-entire types of margins less numerous than they are in the uplands of southern and southeastern Brazil, but they differ from them in showing obvious signs of reduction. Similar contrasts have been observed between the plants of the uplands and the lowlands of India, Hawaii, Ceylon, and other tropical and subtropical areas.

The correlations between leaf-margin and environment would undoubtedly be even more striking, if it were possible to study the "vegetation" of the temperate and tropical zones rather than their "flora." That is to say, if it were possible to deal with numbers of individuals rather than species. For example, the few entire-leaved woody plants in non-xerophytic cold-temperate environments and the comparatively limited number of non-entire woody species in lowland-tropical regions are represented in most cases by a relatively limited number of individuals. Those typical cold-temperate and tropical species that are most important numerically have, except in a few instances, leaves and leaflets with entire margins in lowland-tropical regions and non-entire margins in mesophytic cold-temperate ones.

A second point that deserves consideration, in a discussion of the significance of the percentages given in Table I, is the difference in the relative adaptability of trees, shrubs, and herbs. Arborescent plants, owing to their large size and persistent aerial stems, are more directly exposed to prevailing climatic influences than are small shrubs and herbs. They are, therefore, less adaptable, and, owing to a longer interval between seed germination and seed production, can migrate less rapidly. Herbs, in marked contrast to trees, are the most adaptable and variable type of vegetation. This is due, in part to their small size which enables them to take advantage of local variations in environment, in part to the brevity of their life cycle which increases their opportunity for migration and variation, and largely to the fact that they can avoid periods of unfavorable climatic conditions underground or as small resistant seeds. Thus, although the bulk of herbaceous Dicotyledons are in all probability of comparatively recent origin, they have migrated very rapidly and have established themselves in most regions of the earth.[3]

It is not at all suprising, therefore, that the correlations between leaf-margin and climate are somewhat less strikingly shown among small shrubs and herbs than they are among arborescent species. In tropical lowlands, the smaller plants can escape the full effects of intense heat and sunlight; and it is significant that non-entire species are usually small trees, shrubs, climbing plants, and herbs, many of which occur in protected, comparatively cool habitats. On the other hand, the leaves of the dominant Dicotyledons of tropical forests are almost always entire. Within the temperate zones, not only do small shrubs and herbs live in those arid and unfavorable environments where arborescent plants are of infrequent occurrence, but in mesophytic situations may avoid the full effects of climatic influences to which large trees and shrubs are directly exposed. Of course, herbaceous types may appear above ground only during the warmer or moister seasons of the year.

In view of these facts, it appears to be highly improbable that the present distribution of entire and non-entire Dicotyledonous leaves and leaflets is largely due to factors of heredity rather than those of environment. If leaf form is little subject to modification by environment and is very firmly held on by heredity, the existing ratios between the two types of leaf-margins must have been determined by the original location, subsequent migrations, etc., of those families or groups of Dicotyledons that developed entire and non-entire leaves and leaflets. But, as is shown in the next table, the majority of the families of the Dicotyledons possess both types of foliage. Furthermore, in the distribution of the woody representatives of Dicoty-

[3] Sinnott, E. W. and Bailey, I. W. The origin and dispersal of herbaceous Angiosperms. Annals of Botany **28**: 547–600. 1914.

TABLE IV[4]

	Woody Non-entire	Woody Entire	Herbs Non-entire	Herbs Entire
Piperaceae		150		94
Salicaceae	136	20		
Juglandaceae	16	5		
Betulaceae	28			
Fagaceae	49	56		
Urticales	174	80	130	52
Proteales	321	391		
Olacaceae		69		
Aristolochiaceae		21	1	72
Polygonaceae	2	91	22	350
Chenopodiaceae	2	153	91	207
Amarantaceae	1	83	3	248
Nyctaginaceae		56	3	30
Phytolaccaceae		13		23
Portulacaceae		5		60
Caryophyllaceae		109	7	966
Ranunculaceae	48	5	530	95
Berberidaceae	30	3	12	
Menispermaceae		75	2	1
Magnoliaceae	1	36		
Anonaceae		279		
Myristicaceae		74		
Monimiaceae	11	9		
Lauraceae	1	554	1	2
Papaveraceae			106	
Cruciferae	24	120	808	558
Resedaceae	2	3	31	30
Crassulaceae	6	57	46	200
Saxifragaceae	79	10	129	55
Pittosporaceae	9	33	8	
Cunoniaceae	17			
Hamamelidaceae	9	10		
Rosaceae	479	187	307	22
Connaraceae		70		4
Leguminosae	13	3,329	243	2,339
Geraniaceae	63	4	294	33
Oxalidaceae		8	8	388
Linaceae		25	2	59
Zygophyllaceae	4	30	3	50
Rutaceae	77	434	20	41
Simarubaceae	6	45		
Burseraceae	2	38		
Meliaceae	21	176		
Malpighiaceae	3	256		
Polygalaceae		126		160
Euphorbiaceae	445	514	128	188
Coriariaceae		37		
Celastraceae	107	51		
Anacardiaceae	49	154		

[4] Based upon analyses of the floras of the following regions: E. C. North America, West Indies, Brazil, Patagonia, England, Spain, Flora Orientalis, Flora Capensis, western Australia, East Indies, Simla.

TABLE IV—*Continued.*

	Woody Non-entire	Woody Entire	Herbs Non-entire	Herbs Entire
Aquifoliaceae	28	30	....	....
Aceraceae	17	1	....	....
Sapindaceae	236	172	10	....
Rhamnaceae	70	151	....	....
Vitaceae	109	7	4	....
Tiliaceae	114	38	33	....
Malvaceae	162	58	300	12
Sterculiaceae	202	132	20	1
Dilleniaceae	56	58	8	....
Ochnaceae	53	20	....	....
Marcgraviaceae	....	15	....	....
Guttiferae	....	94	....	....
Dipterocarpaceae	3	69	....	....
Cistaceae	....	96	....	31
Bixaceae	93	21	....	....
Violaceae	47	16	115	22
Flacourtiaceae	10	11	....	....
Passifloraceae	22	18	33	33
Begoniaceae	25	1	63	1
Thymeleaceae	....	111	....	3
Eleagnaceae	....	16	....	....
Lythraceae	1	84	....	101
Rhizophoraceae	....	21	....	....
Combretaceae	....	111	....	....
Myrtaceae	34	1,613	....	....
Melastomataceae	49	253	7	9
Oenotheraceae	6	16	94	78
Araliaceae	39	37	....	5
Umbelliferae	41	9	1,195	219
Cornaceae	4	41	....	....
Ericaceae	89	813	....	....
Myrsinaceae	35	107	....	....
Primulaceae	....	1	69	91
Plumbaginaceae	1	105	5	101
Sapotaceae	....	115	....	....
Ebenaceae	....	78	....	....
Symplocaceae	24	1	....	....
Styracaceae	6	31	....	....
Oleaceae	17	69	....	....
Apocynaceae	....	272	....	15
Asclepiadaceae	....	623	....	207
Convolvulaceae	43	193	102	268
Polemoniaceae	....	....	15	28
Borraginaceae	21	153	27	531
Verbenaceae	182	118	53	26
Labiatae	310	138	1,067	224
Solanaceae	29	150	100	67
Scrophulariaceae	113	113	884	396
Bignoniaceae	16	294	3	....
Gesneriaceae	49	53	60	17
Acanthaceae	47	182	40	232
Myoporaceae	10	24	....	....
Plantaginaceae	....	4	49	71

TABLE IV—*Continued.*

	Woody Non-entire	Woody Entire	Herbs Non-entire	Herbs Entire
Rubiaceae	4	1,261	2	610
Caprifoliaceae	39	59	8	7
Valerianaceae	1	1	70	26
Dipsacaceae	1	....	119	33
Cucurbitaceae	4	....	253	33
Goodeniaceae	14	15	38	28
Compositae	845	1,196	3,164	1,471

ledonous families, there is in almost all cases an obvious correlation between leaf form and environment. For example, such typical entire leaved woody groups as the Anonaceae, Lauraceae, Ebenaceae, Guttiferae, Rhizophoraceae, Myristicaceae, Sapotaceae, Apocynaceae, etc., are practically absent from mesophytic cold-temperate regions, as are such characteristically non-entire families as the Betulaceae, Aceraceae, Platanaceae, etc., from lowland-tropical areas. Particularly significant, however, is the distribution of those families, Malvaceae, Rosaceae, Ulmaceae, Fagaceae, Tiliaceae, Leguminosae, etc., which possess both types of leaf-margins. The non-entire types usually reach their optimum development in mesophytic temperate, cool upland, or equable environments, the entire types in lowland-tropical or physiologically dry habitats, and the transitional forms in intermediate environments. To endeavor to explain all these correlations between leaf form and environment as mere coincidences would be very difficult. When it is taken into consideration, accordingly, that correlations between leaf form and environment occur in numerous families, genera, and even species, and in all parts of the tropical, temperate, and frigid zones, the effects of environment are clearly demonstrated.

Although the form of the leaf-margin of Dicotyledons appears to be very strongly influenced by environment, historical factors and those influences of heredity which tend to maintain existing characters, are, of course, by no means inoperative. In any region, not all species will have been subject to the effects of prevailing climatic conditions for equal lengths of time or an equal number of generations; nor is it necessary to suppose that all species or groups of plants will respond with equal rapidity or in an exactly similar manner to influences of environment. Thus, the limited number of non-entire leaved types in lowland-tropical environments and the comparatively few entire-leaved species in mesophytic cold-temperate regions may be types which (1) have avoided the customary effects of prevailing climatic and edaphic influences by hidden ecological or physiological means, or (2) have been subjected to the modifying influences of a new habitat for too limited a period of time for factors of environment to neutralize those of heredity (as, for example, natural selection tending, more or less rapidly, to eliminate unfavorable forms; variations produced by heterogenesis, orthogenesis, or the inheritance of acquired characters).

Numerous illustrations of the effects of historical factors, such as migration, isolation, etc., have been encountered in tracing the distribution of the two types of leaf-margins. For example, the low percentages of entire-leaved arborescent plants in cold-temperate Eurasia, as compared with similar regions in North America, are due in all probability to the extermination of many of these forms during the glacial period; and to the fact that mountain ranges and other barriers have prevented southern types from migrating northward.

In this connection, it is interesting to note the following comparison between the native plants and the naturalized exotics that are recorded in Britton and Brown's flora of the northern United States and Canada. Here are included species from as far south as southern Virginia, Kentucky, and Kansas. The close similarity between the percentages in the two floras seems to indicate that the effects of the glacial period have been largely neutralized in North America.

Table V

Britton and Brown's Flora (2,365 Native Species)			Britton and Brown's Flora (501 Naturalized Exotics)		
	Percent	Entire, Percent		Percent	Percent
Trees	6	24	Trees	3	16
Shrubs	14	35	Shrubs	7	44
Herbs	80	49	Herbs	90	42

As might naturally be expected, historical influences play a more important role in intermediate types of environments. For example, the high percentages of entire leaved woody plants in Tasmania and southern Australia, Table I, may be due in part to environment, but it should be remembered that these regions have been long isolated, and are not in close contact with extensive mesophytic cold-temperate regions as are the warm-temperate areas of the northern hemisphere.

Among herbaceous plants, historical factors appear to have had a more important effect upon the distribution of the two principal types of leaf-margins than they have among arborescent and shrubby Dicotyledons. This seems to have been due to the fact that, owing to the fundamental differences between these growth forms, herbaceous plants are less subject to or react differently toward prevailing environmental influences; and to the more recent origin and rapid dispersal of herbs.

What then is the physiological significance of the entire and of the non-entire types of Dicotyledonous leaf-margins? Are they actually of vital functional importance or merely necessary concomitants of certain types of foliar structure? This is clearly a problem for anatomical and experimental investigation, and will be considered separately in a subsequent paper. However, there are one or two suggestive facts that should be noted at this time. The serrations, dentations, etc., of non-entire leaves, which are often more conspicuous in the earlier than in the later stages of the ontogeny of the leaf, are frequently glandular or provided with hydathodes or water stomata. The structure and possible excretory function of the non-entire leaf-margin, therefore, deserve careful investigation.

Among woody plants, well-developed non-entire margins occur commonly on comparatively thin, soft leaves with prominent veins. Entire margins, on the other hand, usually occur on thicker, stiffer, more leathery leaves which are provided with structures that seem to retard evaporation and transpiration. The possibility suggests itself, accordingly, that the form of the leaf-margin may be largely influenced, either directly or indirectly, by phenomena of evaporation and transpiration. In those environments where non-entire margins reach their optimum development, the leaves can draw upon abundant soil moisture and transpire freely.[5] In alpine and arctic regions, bogs, steppes, prairies, moors, arid, and saline habitats the leaves of most plants with persistent aerial stems and of many herbaceous forms are exposed to conditions of physiological drought, and are subject to the grave danger of excessive transpiration and evaporation.

If this is the case, why are there such high percentages of entire-leaved plants in tropical rainforests and in other moist tropical

[5] It is interesting to note that in regions with marked alternating periods of heat and cold or dry and wet seasons, the evergreen foliage may be entire when the deciduous types are strikingly non-entire.

environments? Although the leaves of woody plants in such situations are comparatively large, they appear to be somewhat xerophilous in structure. The possible necessity for the reduction of transpiration in even the most humid of lowland-tropical rainforests is indicated by the extreme effects upon foliage of even a few hours' exposure to the full intensity of tropical sunlight. Schimper states:[6] "Every visitor to the botanic gardens at Buitenzorg knows that many plants, during the later hours of the generally sunny forenoon, usually exhibit clear signs of incipient wilting; this continues to increase rapidly until the occurrence of the afternoon shower of rain, by which time many leaves hang down quite in a drooping condition, although they are not unprovided with contrivances against transpiration. During my visit to Buitenzorg in the midst of the rainy season, fourteen rainless sultry days passed in rapid succession, and the vegetation presented a parched appearance such as would hardly have arisen in Europe after a period three times that length. The air remained very moist throughout this dry period, and, in a less sunny climate, the rich nightly dew would not have been so ineffective."

Although the usual effect of the danger of excessive transpiration seems to be to produce xerophilous leaves with entire margins, there are a number of apparent exceptions to this rule. In the sclerophyllous woodlands of warm-temperate regions, the marked tendency for the reduction in leaf surface may result (*Proteaceae*, *Cunoniaceae*, *Quercus ilex* L., *Prunus ilicifolia* Walp., etc.) in the development of highly specialized spinosely toothed, pinnatifid, or deeply divided, leathery leaves. Furthermore, certain of the softer leaved xerophytes, that are protected against excessive transpiration by hairy coverings of various sorts, have non-entire margins.

Pinnatifid or deeply divided leaves, which are of comparatively infrequent occurrence among woody plants, are more common among herbs, and occur to some extent in more or less physiologically dry habitats. In such situations, however, they usually differ from their close relatives in mesophytic habitats in having fewer or no irregularities, serrations, dentations, etc., on the margins of their lobes and sinuses.

Having studied the distribution of entire and of non-entire leaves and leaflets in existing Dicotyledonous floras, it is desirable to examine

[6] Schimper, A. F. W. Plant Geography, p. 220, English Edition, Clarendon Press, Oxford, 1903.

a few Cretaceous and Tertiary floras. As is well known, herbaceous Dicotyledons are of very infrequent occurrence as fossils below the upper Tertiary. In fact, the bulk of the leaves, of which we have a fossil record, seem to have belonged to arborescent or comparatively large woody species. Therefore, a study of the leaf-margins of Cretaceous and of Tertiary floras of Dicotyledons should afford a rough index of the general climatic conditions which prevailed in the region where the floras existed.

TABLE VI

Tertiary Floras

	Entire, Percent
Florissant, Kirchner, Upper Miocene	33
Green River, Lesq., Upper Eocene	29
John Day Basin, Knowlton, Upper Eocene	28
Spitzbergen, Heer, Upper Eocene	46
Arctic, Heer, Upper Eocene	29
Bad Lands, Lesq., Lower Eocene	29
Wilcox, Berry, Lower Eocene	83

Cretaceous Floras

	Entire, Percent
Montana, Knowlton	62
Patoot, Arctic, Heer	51
Atane, Arctic, Heer	81
Dakota, Lesq	54
Raritan, Berry	71

A comparison of the first six Tertiary percentages, given in this table, with those of modern floras indicates very clearly the general temperate character of the climates that prevailed in the regions where these fossil floras existed. Similarly, the percentages of non-entire leaves in the Patoot and Dakota Cretaceous formations denote conditions intermediate between those of typical lowland-tropical and mesophytic cold-temperate climates. The Wilcox flora which, as has been shown by Berry, was a tropical strand flora, is in marked contrast to the more northern or temperate Tertiary floras. The high percentages of entire-leaved forms (megaphyllous) in the Atane beds points to the tropical character of the climate that existed in certain arctic regions during parts of the Cretaceous.

Of course, caution is needed in comparing any percentage in this table with that of a living flora. This is due to the fact that one cannot always be certain that any known fossil flora is a fair sample of the total ancient vegetation of which it once formed a part. Furthermore, the entire-leaved portion of a flora may contain a greater or less number of large- and small-leaved types, depending upon the exact nature of the climatic and edaphic influences that may have been operative. Therefore, in comparing fossil with living floras, it is important to take into consideration the number of megaphyllous and of microphyllous types that are represented. It should be noted, however, that this method of studying the climates of the Cretaceous and Tertiary rests upon a physiological and ecological basis rather than upon the usual phylogenetic one. It promises to afford a simple and rapid means of gauging the general climatic conditions of the Cretaceous and Tertiary, and of checking the accuracy of conclusions derived from other lines of evidence.

In conclusion, it may well be asked, what bearings this study of the distribution of entire and non-entire leaves and leaflets has upon the question of the relative conservatism of the leaf? As far as the leaf-margin of Dicotyledons is concerned, it may be very variable or extremely inconstant. For example, so long as entire-leaved plants remain in habitats that strongly favor the formation of entire margins, foliar form will remain unaltered, and the leaf will appear to be quite conservative. The most variable conditions, on the other hand, seem to occur in intermediate environments, or among entire leaved plants in non-entire environments, or *vice versa*.

It cannot be too strongly emphasized that there is grave danger in inferring that, because a certain character has remained unaltered in one or more groups of plants through long periods of geological time or has varied greatly among certain closely related forms, the organ which possesses it is inherently "conservative" or "inconstant." In any organ, not all characters are necessarily equally stable or variable. Furthermore, the same character may vary in its constancy or instability in different environments, in different plants, and at different stages in the ontogeny of the individual or in the phylogeny of the genus or family. Although characters of little or no apparent functional importance have been shown in certain cases to be more conservative than others, that are subject to the influences of environment, it should be kept in mind that a functionally important character may long remain unaltered, if it is subjected to an unchanging environment. Continuity of similar environmental influences is responsible, in all probability, for some of the most striking cases of the persistence of Dicotyledonous foliar types from the Cretaceous to the present.

The problem of the relative conservatism of the various organs or parts of plants is such an exceedingly complicated one, that it deserves careful experimental investigation.

Summary

There is a very clearly marked correlation between leaf-margin and environment in the distribution of Dicotyledons in the various regions of the earth.

Leaves and leaflets with entire margins are overwhelmingly predominant in lowland-tropical regions; those with non-entire margins in mesophytic cold-temperate areas.

In the tropical zones, non-entire margins are favored by moist uplands, equable environments, and protected, comparatively cool habitats; in the cold-temperate zones, entire margins are favored by arid environments and other physiologically dry habitats.

Correlations between leaf-margin and prevailing climatic influences are more strikingly shown among trees and large shrubs than among herbs, as might naturally be expected, when the fundamental differences between these important growth forms are taken into consideration.

The determination of the percentages of entire and of non-entire leaves in Cretaceous and Tertiary Dicotyledonous floras, affords a simple and rapid means of gauging the general climatic conditions which existed in the regions where these plants flourished.

There is grave danger in inferring, because a certain foliar character has remained unaltered through long periods of geological time, or has varied greatly among closely related forms, that the leaf is inherently "conservative" or "inconstant."

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