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ART. XXVI.—*The Pertinacity and Predominance of Weeds;* by ASA GRAY.

A WEED is defined by the dictionaries to be "Any useless or troublesome plant." "Every plant which grows in a field other than that of which the seed has been [intentionally] sown by the husbandman is a weed," says the Penny Cyclopædia, as cited in Worcester's Dictionary. The Treasury of Botany defines it as "Any plant which obtrusively occupies cultivated or dressed ground, to the exclusion or injury of some particular crop intended to be grown. Thus, even the most useful plants may become weeds if they appear out of their proper place. The term is sometimes applied to any insignificant-looking or unprofitable plants which grow profusely in a state of nature; also to any noxious or useless plant." We may for present purposes consider weeds to be plants which tend to take prevalent possession of soil used for man's purposes, irrespective of his will; and, in accordance with usage, we may restrict the term to herbs. This excludes predominant indigenous plants occupying ground in a state of nature. Such become weeds when they conspicuously intrude into cultivated fields, meadows, pastures, or the ground around dwellings. Many are unattractive, but not a few are ornamental; many are injurious, but some are truly useful. White Clover is an instance of the latter. Bur Clover (*Medicago denticulata*) is in California very valuable as food for cattle and sheep, and very injurious by the damage which the burs cause to wool. In the United States, and perhaps in most parts of the world, a large majority of the weeds are introduced plants, brought into the country

directly or indirectly by man. Some—such as Dandelion, Yarrow, and probably the common Plantain and the common Purslane—are importations as weeds, although the species naturally occupy some part of the country.

Why weeds are so pertinacious and aggressive, is too large and loose a question: for any herb whatever when successfully aggressive becomes a weed; and the reasons of predominance may be almost as diverse as the weeds themselves. But we may enquire, whether weeds have any common characteristic which may give them advantage, and why the greater part of the weeds of the United States, and probably of similar temperate countries, should be foreigners.

As to the second question, this is strikingly the case throughout the Atlantic side of temperate North America, in which the weeds have mainly come from Europe; but it is not so, or hardly so, west of the Mississippi in the region of prairies and plains. So that the answer we are accustomed to give must be to a great extent the true one, namely, that, as the district here in which weeds from the Old World prevail was naturally forest-clad, there were few of its native herbs which, if they could bear the exposure at all, were capable of competition on cleared land with emigrants from the Old World. It may be said that these same European weeds, here prepotent, had survived and adapted themselves to the change from forest to cleared land in Europe, and therefore our forest-bred herbs might have done the same thing here. But in the first place the change must have been far more sudden here than in Europe; and in the next place, we suppose that most of the herbs in question never were indigenous to the originally forest-covered regions of the Old World; but rather, as western and northern Europe became agricultural and pastoral, these plants came with the husbandmen and the flocks, or followed them, from the woodless or sparsely wooded regions farther east where they originated. This, however, will not hold for some of them, such as Dandelion, Yarrow, and Ox-eye Daisy. It may be said that our weeds might have come to a considerable extent from the bordering more open districts on the west and south. But there was little opportunity until recently, as the settlement of the country began on the eastern border; yet a certain number of our weeds appear to have been thus derived: for instance, *Mollugo verticillata*, *Erigeron Canadense*, *Xanthium*, *Ambrosia artemisiæfolia*, *Verbena hastata*, *V. urticifolia*, etc., *Veronica peregrina*, *Solanum Carolinense*, various species of *Amarantus* and *Euphorbia*, *Panicum capillare*, etc. Of late, and in consequence of increased communication with the Mississippi region and beyond—especially by rail-roads—other plants are coming in to the Eastern States as weeds, step by step, by

somewhat rapid strides; such as *Dysodia chrysanthemoides*, *Matricaria discoidea*, *Artemisia biennis*. Fifty years ago *Rudbeckia hirta*, which flourished from the Alleghanies westward, was unknown farther east. Now, since twenty years, it is an abundant and conspicuous weed in grass-fields throughout the Eastern States, having been accidentally disseminated with Red-clover seed from the Western States.

There are also native American weeds, doubtless indigenous to the region, such as *Asclepias Cornuti*, *Antennaria margaritacea* and *A. plantaginifolia*, and in enriched soils *Phytolacca decandra*, which have apparently become strongly aggressive under changed conditions. These are some of the instances which may show that predominance is not in consequence of change of country and introduction to new soil.

In many cases it is easy to explain why a plant, once introduced, should take a strong and persistent hold and spread rapidly. In others we discern nothing in the plant itself which should give it advantage. *Lespedeza striata* is a small and insignificant annual, with no obvious provision for dissemination. It is a native of China and Japan. In some unexplained way it reached Alabama and Georgia and was first noticed about thirty-five years ago; it has spread rapidly since, especially over old fields and along road-sides, and it is now very abundant up to Virginia and Tennessee, throughout the middle and upper districts, reaching even to the summits of the mountains of moderate elevation. In the absence of better food it is greedily eaten by cattle and sheep. The voiding by them of undigested seeds must be the means of dissemination; but one cannot well understand why it should spread so widely and rapidly, and take such complete possession of the ground. It is one of the few weeds which are accounted a blessing.

Professor Claypole, of Antioch College, Ohio, has recently contributed to the Third Report of the Montreal Horticultural Society (1877–8), an interesting Essay, On the Migration of Plants from Europe to America, with an Attempt to explain Certain Phenomena connected therewith. The phenomena which he would explain are the abundant migration of numerous weeds from Europe to the shore of North America, while others fail to come, and the general failure of North American weeds to invade Europe. We have offered a fairly good explanation of the first. And Professor Claypole goes far toward explaining the second when he notes that seed is (or formerly was) mainly brought from the Old World to the New, and the same may be said of cattle and other emigration; that the cooler and shorter summer of the north of Europe renders the ripening of some seed precarious, etc. He does not mention the fact that American plants by chance reaching

Europe have to compete with a vegetable world in comparatively stable equilibrium of its species, while European weeds coming —or which formerly came—to the United States found the course of nature disturbed by man and new-made fields for which they could compete with advantage. But his ingenious hypothesis is that weeds have a peculiarly "plastic nature, one capable of being moulded by and to the new surroundings," by which the plant "ere long adapts itself, if the change is not too great or sudden, to its new situation, takes out a new lease of life, and continues in the strictest sense a weed;" "that the plants of the European flora possess more of this plasticity, are less unyielding in their constitution, can adapt themselves more readily to new surroundings," and that it is "the lack of this plasticity in the American flora which incapacitates it from securing a foot-hold and obtaining a living in the different conditions of the New World;" that although "in the Miocene era the European and American floras were very much alike," yet "since that era the European flora has been vastly altered, while the American flora still retains a Miocene aspect, and is therefore the elder of the two;" "that this long persistence of type in the American flora may have induced, by habit, a rigidity or indisposition to change;" that "the European is thus better able to adapt itself to the strange climate and conditions—that is, to emigrate—than the American:" and thus, being more plastic or adaptable it succeeds in the New World, while the less adaptable American flora fails in the Old World."

So far as we know, the greater plasticity of European as compared with American plants is purely hypothetical. "More plastic" would mean of greater variability, which, if true, might be determined by observation. Because Europe once had more species or types in common with North America than it now has, it does not seem to follow that the former has "a younger plant-life," or that its existing plants are more recent than those of the American flora. And as already intimated, so refined an hypothesis is hardly necessary for the probable explanation of the predominance of Old World weeds in the Atlantic United States.

Mr. Henslow, in his remarkable memoir, On the Self-Fertilization of Plants (which we reviewed in the June number of this Journal) derives from different but equally theoretical premises an opposite conclusion, — namely, that weeds or intrusive and dominant plants in general, and of great emigrating capabilities, have "a longer ancestral life-history than their less aggressive relatives." He also maintains that weeds, and plants best fitted for domination in the manner of weeds, possess a common characteristic to which this dominance may be attributed, namely, that they are in general self-fertilized

plants. A rapid generalizer might find confirmation of this in the converse, which is obviously true, that plants with blossoms very specially adapted for cross-fertilization by particular insects, and therefore dependent on such special aid, are comparatively local and unaggressive; yet some of these are widely distributed. It will also be understood that self-fertilization may give advantage to an intruding plant at the outset, by enabling an exceptionally well-fitted individual to initiate a favored race. And self-fertilization, with its sureness, would always be most advantageous unless cross-fertilization brings some compensatory advantage greater on the whole than that of immediate sureness to fertilize.

But the test of the theory is, whether weeds and emigrating herbs in general are more self-fertilizing or less subject to cross-fertilization than the majority of related plants, and whether many or any of them are actually self-fertilized through a succession of generations. It seemed to us that, in a limited way, the weeds which Europe has given to North America might answer this question. To keep within bounds and to have a case with all the data unquestionable, we will collate the weeds of European parentage which evince a dominating character in the United States east of the Mississippi, referring for the purpose to the Manual of the Botany of the Northern United States and Chapman's Southern States Flora. The latter, however, adds not a single weed from Europe of any predominance. We include only those which have taken a strong hold and become prominent either by their general diffusion over the area or by taking marked possession of certain districts. For examples of the latter take *Echium vulgare* in Virginia, *Ranunculus bulbosus* and *Leontodon autumnale* in Eastern New England, and *Genista tinctoria* which covers certain tracts in the eastern part of Massachusetts, although nearly unknown elsewhere. We must include several species which as weeds came from Europe, although they are probably, some of them undoubtedly, indigenous to some part of the United States.

The following are the herbaceous plants naturalized from Europe and of an aggressive character in the Atlantic United States. Herbs of recent introduction, and those of however ancient naturalization which have not either spread widely or increased greatly over a considerable district, are omitted.

The 18 species in italic type, nearly half of them grasses, are probably indigenous to some portions of North America. In some cases the introduced and the indigenous plants have come into contact.

Ranunculus bulbosus.
Ranunculus acris.
Nasturtium officinale.
Sisymbium officinale.
Brassica Sinipistrum.
Raphanus Raphanistrum.
Capsella Bursa-pastoris.
Reseda Luteola.
Saponaria officinalis.
Silene inflata.
Lychnis Githago.
Stellaria media.
Portulaca oleracea.
Malva rotundifolia.
Genista tinctoria.
Trifolium arvense.
Trifolium agrarium.
Trifolium repens.
Daucus Carota.
Pastinaca sativa.
Conium maculatum.
Tussilago Farfara.
Inula Helenium.
Gnaphalium uliginosum.
Anthemis Cotula.
Achillæa Millefolium.
Tanacetum vulgare.
Leucanthemum vulgare.
Cirsium arvense.
Cirsium lanceolatum.
Lappa officinalis.
Cichorium Intybus.
Leontodon autumnale.
Taraxacum Dens-leonis.
Plantago major.
Plantago lanceolata.
Anagallis arvensis.
Verbascum Thapsus.
Verbascum Blattaria.
Linaria vulgaris.
Mentha viridis.
Mentha piperita.
Calamintha Nepeta.
Calamintha Clinopodium.
Nepeta Cataria.
Nepeta Glechoma.
Marrubium vulgare.
Galeopsis Tetrahit.
Leonurus Cardiaca.
Lamium amplexicaule.
Echium vulgare.
Symphytum officinale.
Echinospermum Lappula.
Cynoglossum officinale.
Solanum nigrum.
Chenopodium album.
Chenopodium hybridum.
Chenopodium Botrys.
Polygonum aviculare.
Polygonum Convolvulus.
Rumex crispus.
Rumex sanguineus.
Rumex Acetosella.
Allium vineale.
Alopecurus pratensis.
Phleum pratense.
Agrostis vulgaris.
Agrostis alba.
Dactylis glomerata.
Poa annua.
Poa compressa.
Poa pratensis.
Poa trivialis.
Eragrostis poæoides.
Festuca ovina.
Festuca pratensis.
Bromus secalinus.
Lolium perenne.
Triticum repens.
Triticum caninum.
Anthoxanthum odoratum.
Panicum glabrum.
Panicum sanguinale.
Panicum Crus-galli.
Setaria glauca.
Setaria viridis.

The plants of this list, regarded as weeds, are of very various character; and several of them, such as White Clover and most of the grasses, where most dominant, do not fall under the ordinary definition of weeds at all, but under that of plants useful to the farmer. Some, like Purslane, are only garden-weeds; some belong to pastures and meadows; others affect road-sides. The fewness of European corn-weeds is remarkable. Chess and Corn-cockle (*Lychnis Githago*) are the only ones on the list. Corn Poppy, Blue-bottle and Knapweed (*Centaurea Cyanus* and *C. nigra*) and Larkspur are conspicuously wanting; but the last two are not wholly unknown in some parts of the country.

But the only question before us is, whether these plants introduced from Europe are or are not self-fertilized, or more habitually so than others, so that this may be accounted an element of their predominance. Apparently this question must be answered in the negative. The question is not whether they are self-fertilizable. The great majority of plants are so, even of those specially adapted for intercrossing. The plants of this list appear to belong to the *juste milieu*. Only one (*Rumex Acetosella*) is completely dicœcious; a few are incompletely dicœcious or polygamous; the two species of *Plantago* are dichogamous to the extent of necessary dioicism or monoicism; a large number of the corolline species are either proterandrous or proterogynous, including two or three anemophilous species,

and all the Grasses (which form the last quarter of the list) are anemophilous and more or less dichogamous, and therefore not rarely cross-fertilized. Of those which are not anemophilous we notice none which are not habitually visited by insects (except perhaps *Gnaphalium uliginosum*), and which therefore are almost as likely to be cross-fertilized as close-fertilized; while in not a few (such as the *Compositæ* generally and most of the other *Gamopetalæ*) the arrangements which favor intercrossing are explicit. There is no cleistogamous and therefore necessarily self-fertilized plant in the list, except *Lamium amplexicaule*, which also cross-fertilizes freely.

In California the prevalent weeds are largely different from those of the Atlantic States and, as would be expected, are mostly of indigenous species or immigrants from South America; yet the common weeds of the Old World, especially of Southern Europe, are coming in. The well-established and aggressive ones, such as *Brassica nigra*, *Silene Gallica*, *Erodium cicutarium*, *Malva borealis*, *Medicago denticulata*, *Marrubium vulgare* and *Avena sterilis*, were perhaps introduced by way of Western South America. They are mostly plants capable of self-fertilization, but also with adaptations (of dichogamy and otherwise) which must secure occasional crossing.

We cannot avoid the conclusion that self-fertilization is neither the cause, nor *a* perceptible cause of the prepotency of the European plants which are weeds in North America.

A cursory examination brings us to a similar conclusion as respects the indigenous weeds of the Atlantic States, those herbs which under new conditions, have propagated most abundantly and rapidly, and competed most successfully in the strife for the possession of fields that have taken the place of forest. The most aggressive of these in the Northern States are *Epilobium spicatum* in the newest clearings, which is dichogamous (proterandrous) to a degree which practically forbids self-fertilization; and in older fields, *Asclepias Cornuti*, which is specially adapted for cross-fertilization by flying insects; *Antennaria plantaginifolia* and *A. margaritacea*, which are dicœcious; and next to these perhaps the two wild Strawberries, then *Erigeron annuum* and *E. strigosum*, with certain Asters and Golden-rods, all insect-visited and dichogamous, and *Verbena hastata*, *urticifolia*, etc.. the frequent natural hybridization of which testifies to habitual intercrossing.

Those who suppose that only conspicuous or odorous flowers are visited by flying insects should see how bees throng the small, greenish, and to us odorless blossoms of *Ampelopsis* or Virginia Creeper and of its Japanese relative.