History of Ecological Sciences, Part 48: Formalizing Plant Ecology, about 1870 to mid-1920s

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A German zoologist, Ernst Haeckel, coined and defined a new branch of biology, "Oekologie," in 1866 (Egerton 2013). In the later 1800s, four ecological sciences emerged: (terrestrial) plant ecology, (terrestrial) animal ecology, limnology, and marine biology. Plant ecology evolved out of phytogeography and physiology (Billings 1985:5–6), to which was added during the 1890s investigations of plant communities and vegetation succession. Physiology was important, but played a relatively passive role: its significance often depending on how well phytogeographers understood it. European botanists and publications led the way. Phytopathology during the 1800s is discussed in part 44 (Egerton 2012) and omitted here. For phytopathology during the early 1900s, see G. C. Ainsworth, *Introduction to the History of Plant Pathology* (1981) and C. L. Campbell et al., *The Formative Years of Plant Pathology in the United States* (1999:225–339). The history of aquatic plant ecology is part of limnology and marine ecology and will be discussed in parts 50 and 51. The ecology of lichens is deferred to part 52 on the history of symbiosis studies. After these exclusions, the remaining plant ecology, about 1870 to mid-1920s, is still vast in scope and detail, and surveys by Becking (1957), Whittaker (1962), Shimwell (1972), Tobey (1981), Nicolson (1989, 1996), and Cittadino (1990) provide introductions to additional developments and literature.

Europe

Phytogeography along ecological lines laid down by Humboldt (Egerton 2009*b*) and Augustin-Pyramus de Candolle (Egerton 2010:26–29) continued throughout the 1800s (Pritzel 1871–1877:458–462, Nicolson 1996) and can be seen in such treatises as Joakim F. Schouw's *Grundtraek til en almindelig Plantgeographie* (1822, German, 1823), Franz Meyen's *Grundriss der Pflanzengeographie* (1836, English 1846, 1977), Arthur Henfrey's *Vegetation of Europe, Its Conditions and Causes* (1852, 1977), and Alphonse de Candolle's *Géographie botanique raisonée* (1855) (Reed 1942:128–129). German botanists led the way, with Russian botanists following a parallel, rather independent, course (Becking 1957:417–419).

An Austrian, Anton Kerner von Marilaün (1831–1898), studied medicine at the University of Vienna, but soon gave up his practice to become a botanist (Kronfeld 1908, Stafleu and Cowan 1976–1988, II:525–530, Nicolson 1996:297–298), who was strongly influenced by Humboldt (Cittadino 1990:119). He became a professor at Budapest, then Innsbruck, and finally in Vienna. While in Hungary he had collected plants in botanically little-known eastern Hungary and Transylvania and published *Das Pflanzenleben der Danaulaender* (1863). Its American translator claimed that this book "is the immediate and direct parent of all later works on Plant Ecology" (Conard 1951:vii). Is this translator merely hyping a work he has translated or is there some validity to his claim? R. J. Goodland (1975:241) reserved that "parental honor" for Warming (1995). Dwight Billings (1985:5) and Malcolm Nicolson (1996:304–305) agreed with Conard. Clearly, Kerner's *Plant Life of the Danube Basin* is a good landmark with which to begin this history.

Kerner complained that a copious literature on plant physiognomy had developed without a standard terminology to describe scientifically all native plant formations. For example (Kerner 1951:5–6, 1977):

> *Whereas Humboldt considers the north German heather-covered coastal plains as steppes, and Koch applies that name to a formation composed of high sod-forming grasses, and Willkomm restricts the term to formations on saline soils of both highlands and lowlands, Grisebach—whose usage of the word steppe we shall follow—conceives of a steppe as a region in which, because of extreme heat, sterility and drought of summer, no tree can survive, and in which the most diverse other formations composed of grasses, herbs, etc., may develop.*

Kerner argued that others had failed to choose as examples definite genera, but had portrayed physiognomic differences on the broadest lines of resemblance. Furthermore, others had used vernacular names as scientific terms. He developed a new terminology, but without resorting to Latin, as Linnaeus had, because the German language was quite adequate for the purpose (Kerner 1951:7). He did not consider that this might be a problem for people who knew no Germanic language. Kerner did not become the Linnaeus of plant ecology, but Patrick Matagne (1998:428) thinks that Kerner's effort "laid the theoretical basis for a transition from phytogeography to phytosociology."

Kerner aspired to describe the origin, development, maturation, and decline of each formation. The general picture seemed clear (Kerner 1951:10, 1977):

> *In bitter struggle with the unyielding elements the first settlers gain possession of the lifeless earth. Step by step they press forward over the waste talus of the mountains or over the shifting sands of coastal plains and clothe them with a sparse plant cover. Years must pass before a second generation can unfold with greater strength and variety on the prepared soil. But ceaselessly plant life works, and builds its green structure greater and greater. On the remains of fallen races the germs of other younger, newer plant forms take root, and so it goes on with tireless change, until at last the shady crowns of a high forest whisper above the deep mull soil.*

The challenge was to unravel these changes and their causes within each formation. As he crossed the Hungarian plains, he could see where a village had stood 200 years previously, because there were nettles there foreign to the prairie flora, which accompany human settlers, and also locusts, oaks, and apparently

Fig. 1. (a) Anton Kerner. Kronfeld 1908:frontispiece. (b) Alphonse de Candolle. (c) August H. R. Grisebach. Magin-Gonze 2004:165, 202.

willows that villagers had planted (Kerner 1951:16). He was particularly interested in explaining why trees could invade the prairie only along rivers or in lowlands covered with fens, and he compared the treeless prairie with the treeless mountains above treeline. In both cases, the season for tree growth was only about two months, limited on the prairie by drought and on mountains by frost (Kerner 1951:26–27). On the other hand, treeless alpine regions had scant prostrate perennial vegetation, but the treeless prairie had abundant vertical annuals. He often could explain the causes of vegetative dynamics, and where he could not, he gave good descriptions of vegetation. Many trees obviously had their seeds distributed by the wind. He was puzzled by oaks. Those growing along streams had their acorns moved by water, but what about those away from streams? He postulated that in past times streams had gone in different directions (Kerner 1951:39–40). Thoreau had published his insight about squirrels burying more acorns than they ever recover during winter, in the Middlesex Agricultural Society's *Transactions* (1860), and republished in the New York *Weekly Tribune* (Egerton 2011:269); neither American publication was likely to reach a botanist in the Austrian Empire. Puzzling acorn dispersal was not a typical example of Kerner's reasoning; his book is indeed an impressive achievement. Probably no one followed his example by writing a similar book on another European region because no one could—until 1904–1908, when Carl Schröter published his *Pflanzenleben der Alpen* (see below).

Instead, conventional phytogeography and physiology progressed in leading European countries. Matagne sees four phytogeographers as most important in the later 1800s—Kerner, Alphonse de Candolle, Grisebach, and Flahault—extracts from whose works Matagne reprinted following his introductory essay (in Acot 1998:439–519). Swiss Alphonse de Candolle (1806–1893) continued the great work of his father, Augustin-Pyramus de Candolle (Pilet 1971*a*, *b*, Stafleu and Cowan 1976–1988, I:433–452, Dajoz 1984:39–46, Drouin 1993:60–62, Isley 1994:178–180, Matagne 1998:432–433, Magnin-Gonze 2004:165–167, Egerton 2010:26–29), which culminated in his *Géographie botanique raisonée* (two volumes, 1855). He corresponded with Charles Darwin and Hewett Watson, among others. Candolle judged heat and moisture to be the dominant factors affecting plant distribution. Matagne

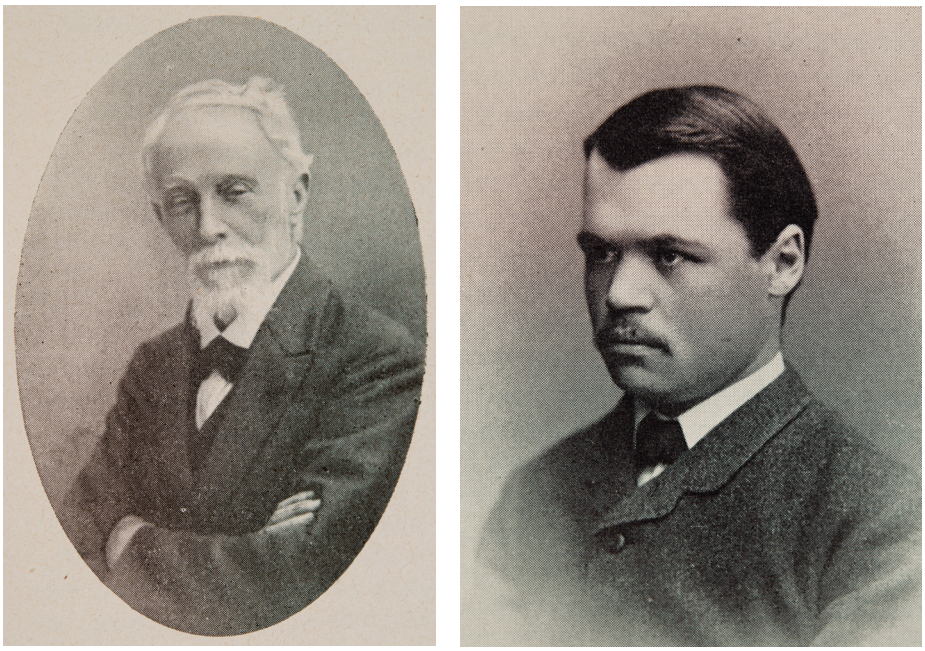


Fig. 2. (a) Charles-Henri-Marie Flahault. Virville 1954:247.
(b) Ragnar Hult. Collander 1965: plate 4.

(1998:433) thinks Candolle's development of a classification based on plants' mode of life contributed to the emergence of a new ecological approach, centering on plant–environmental interactions (published before Kerner's classification). Nicolson (1996:300) viewed Alphonse de Candolle as more of a floristic phytogeographer than as a follower of Humboldt.

German August Heinrich Rudolf Grisebach (1814–1879) was a professor of botany at the University of Göttingen, influenced by Humboldt, who studied taxonomy as a basis for his phytogeography (Reed 1942:131, Wagenitz 1972, Stafleu and Cowan 1976–1988, I:1007–11, Morton 1981:433, Cittadino 1990:113–114, 119–122, Matagne 1998:429–431, Magnin-Gonze 2004:202). He traveled widely in Europe, but not elsewhere. His numerous publications (five early ones are reprinted in Egerton 1977*b*), culminated in his authoritative *Die Vegetation der Erde und ihrer klimatschen Anordnung* (two volumes, 1872, French, 1877).

French botanist Charles-Henri-Marie Flahault (1852–1935) received his doctorate at Paris in 1878, then traveled with botanist Gaston Bonnier (1853–1922) to Sweden to study the relationship of plants and climate (Emberger 1936, Jovet 1954:256–257,Stafleu and Cowan 1976–1988, I:843, Matagne 1998:434–437, 1999:49–50). Bonnier and Flahault's "Observations sur les modifications des végétaux suivant les conditions physiques du milieu" (1878) compared the similarities and differences between alpine and polar climates and plants, somewhat reminiscent of Kerner's comparisons (1863) of treeless alpine and prairie regions and plants. Flahault returned to Sweden on four occasions and became friends with Warming. Flahault lived through the period of transition in which plant ecology evolved from

earlier disciplines, and he participated in the progress, while remaining a phytogeographer. He accepted the chair in botany at Montpellier in 1881 and occupied it for 47 years. In 1891 he started a school of Mediterranean phytogeography (Matagne 1999:169–171), and in 1897 he sent to the Académie des Sciences six maps on the phytogeography of the French coastal region, which were not published until 1937.

Another persistent subject of investigation was plant succession (Clements 1916:8–32, Egerton 2009). Norwegian Professor of Botany Alex Blytt, at Kristiana (Oslo), in 1876 and later, continued investigations of paleo-vegetational history, pioneered by Japetus Steenstrup (1842, Fries 1950:70, Egerton 2009:49–52), after documentation of the waxing and waning of ice ages provided an opportunity to understand causes of vegetational changes; his conclusions were controversial at the time (Clements 1916:21–22, 382–384). Finnish botanist Ragnar Hult (1857–1899) studied at Uppsala University before receiving his doctorate in 1881 from Helsingfors University (Fries 1950:70, Collander 1965:74–77, Stafleu and Cowan 1976–1988, I:361). His dissertation was on the physiognomy of northern Ostrobothnia and Kemi-Lappmark, in which he distinguished seven vegetation layers. His stratification system was later modified by Sernander and is now known as the Hult-Sernander scale of cover (Becking 1957:415, 419–420). Hult's most important work analyzed "Blekinges Vegetation" (1885) in southern Sweden. This study on the developmental history of Blekinge's plant communities "first fully recognize[d] the fundamental importance of development in vegetation," and made "a systematic study of a region upon this basis" (Clements 1916:22). Hult "traced the succession of each intermediate formation through its various stages to the supposed climax." Clements provided an English summary of Hult's Swedish-language study, and Nicolson (1996:303) quotes passages translated by Sigridur Oladottir. Becking (1957:415) stated that "Hult (1881) published, for the first time, a complete species list with numerical evaluation of cover degree." In summer 1886, Hult taught a field course in plant geography, taken by Swedish student Rutger Sernander, who "adopted Hult's ideas with great enthusiasm" (Fries 1950:70–71, Collander 1965:77). Sernander is discussed below.

In the 1890s, three botanists guided the transition from phytogeography to plant ecology: Germans Drude and Schimper and a Dane, Warming (Reed 1942:132–134, Magnin-Gonze 2004:203). (Carl Georg) Oscar Drude (1852–1933) studied under Grisebach and received his doctorate from Göttingen in 1873 (Stafleu and Cowan 1976–1988, I:682–683, Matagne 2009: see index). Drude apparently did not know Haeckel's term "oecologie" when he published *Handbuch der Pflanzengeographie* (1890, 1977), and his *Handbuch* was little known in America until after he published *Deutschlands Pflanzengeographie* (1896), which received an eager audience at the University of Nebraska, mainly from Roscoe Pound and Frederic Clements, who were conducting a botanical survey of Nebraska (Tobey 1981:63–64, McIntosh 1985:28, Nicolson 1989:153–154). Drude provided them with a set of definitions, including "habitat" and "formation," and "a somewhat mechanical theory relating physical and biological factors" that could account for geographical distribution of species. When they obtained Drude's *Handbuch*, however, they found his vegetational boundaries of the Great Plains inaccurate (Kendeigh 1954:158). "Schouw (1823) proposed a qualitative arrangement of species into groups of 'plantae sociales, gregariae, copiosae, sparsae and solitarine', in which Drude (1890) followed him" (Becking 1957:415). Drude was active in Germany during its flourishing empire, when maps were very important, and he was able to exploit that interest for plant geography maps (Gütler 2011).

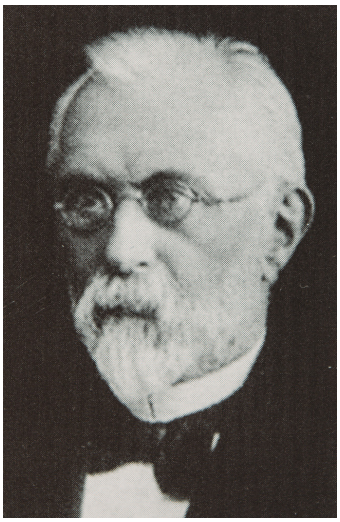


Fig. 3 (a) C. G. Oscar Drude. Web site. (b) Karl F. Schimper. Schimper 1903: frontispiece. (c) J. Eugenius B. Warming. Web site.

The first botanist known to have used "oecologie" in print was H. Reiter, *Die Consolidation der Physiognomick als Versuch einer Oekologie der Gewaechse* (1885). In 1893, the term "ecology" was introduced to two English-speaking audiences: by animal physiologist and professor of medicine John Burdon-Sanderson (1828–1905) in his presidential address (1893:465) to the British Association for the Advancement of Science, and by a Committee on Terminology of Physiology at the Madison Botanical Congress (McIntosh 1985:29). However, not until publication of Warming's *Plantesamfund: Grundträk af den okologiske Plantesgeografi* (1895, German 1896; extracts from both editions reprinted in Acot 1998, II:827–901). Warming substantially revised his book for the English edition (1909, 1977), utilizing literature that had appeared since 1895, including Schimper's *Pflanzengeographie* (1898). (Johannes) Eugenius (Bülow) Warming (1841–1924) was from a Frisian island in the North Sea (Christensen 1924–1926, I:617–665, 776–806, Rosenvinge et al. 1927, Müller 1976, Isley 1994:227–229, Matagne 2009: see index). While a student at the University of Copenhagen, he spent three years, 1863–1866, as secretary to a Danish zoologist in Brazil, where Warming studied the flora (Goodland 1975). He received a Ph.D. from the University of Copenhagen in 1871, and he taught in Stockholm, 1882–1885. He became professor of botany and director of the botanic garden at the University of Copenhagen, 1886–1911. Müller (1976) called Warming "founder of plant ecology," and Pascal Acot (1998:675) states: "Historians of biology concur that [*Plantesamfund*] marked the birth of scientific ecology." (Billings 1985:5 and Nicolson 1996:304–305 cited instead Kerner 1863.)

Andreas Schimper (1856–1901) was the son of botanist Wilhelm Schimper, director of the Strasbourg Natural History Museum and, after the Franco-Prussian War, Professor of Natural History at the

University of Strasbourg. Andreas received his doctorate in natural philosophy from that university in 1878, then studied under Julius Sachs at Würzburg (Sanders 1975, Cittadino 1990:97–115, Isley 1994:271–273, Matagne 2009: see index). He traveled in North and South America, and in Brazil he studied the symbiotic relationship between ants and *Cecropia* trees (Schimper 1888). He died in Basel, Switzerland, age 45, from diabetes and from malaria contracted earlier along the African coast. He was a prolific author. For ecology, his most important work was *Pflanzengeographie auf physiologischer Grundlage* (1898, English, 1903, 870 pages, 502 illustrations, and 4 color maps)—one of the largest ecology monographs written by one author (surpassed much later by G. E. Hutchinson's four-volume *Treatise on Limnology*). It illustrates the synthesis of phytogeography and physiology that became the foundation of plant ecology. In his preface, Schimper stated (1903:vi) that "The connexion between the forms of plants and the external conditions at different points on the earth's surface forms the subject-matter of oecological plant-geography," and that Grisebach's point of view had become obsolete! Schimper identified a schism in biogeography that persisted well into the 1900s (Worster 1977:194–195, Hagen 1986). Schimper credited Haeckel for naming this ecological science "of biological adaptations." Cowles (1909:356) judged Schimper "a prophet as well as an ecologist of the first magnitude." However, Schimper borrowed heavily from Warming, with scant acknowledgment (Goodland 1975:243).

Warming and Schimper's books were more complementary than duplicative (Dajoz 1984:108–111). Schimper's was encyclopedic and well illustrated with many photographs and drawings. Warming's book is more like a textbook, with no illustrations, and half the size of Schimper's. Both books were worldwide in scope, differing in that respect from Kerner's. Warming's chapter 3 (1909:12–13), only 1.5 pages, might be the earliest general discussion of plant communities. It is brief because it is meant to orient one's thinking to the following chapters on different kinds of plant communities. Equally brief is chapter 24 (Warming 1909:83–84), "Symbiosis of Plants with Animals," which merely identifies different kinds of symbiotic relationships, without describing or explaining them. Chapter 25 (Warming 1909:84–91), "symbiosis of plants with one another, mutualism" is more detailed, discussing parasitism, helotism (fungi), mycorhiza and endophytes, epiphytes, saprophytes, and lianes. Chapter 26 (Warming 1909:91–95), "Commensalism, plant-communities," discusses plants that have an aggregate existence but no interactions except a common struggle for life requirements. A historian of symbiosis, Jan Sapp (1994:30) faults Warming for only devoting nine pages to the subject, but if one counts all the pages in Section II, "Communal Life of Organisms," (chapters 22–26), it is 14 pages, and Warming mentioned many biologists who had published on the subject. Sapp also faults him for too strong an emphasis on struggle for existence and skepticism about reciprocity between species. Chapter 34 (Warming 1909:131–136), "Oecological classification," divides formations into 13 groups, each of which are discussed in following chapters: hydrophytes, helophytes, oxylophytes, psychrophytes, halophytes, lithophytes, psammophytes, chersopohytes, eremophytes, psilophytes, sclerophyllous, coniferous, and mesophytes. If some of these terms are unfamiliar to modern readers, it shows that not all of Warming's suggested terms were adopted by other plant ecologists. Chapter 35 (Warming 1909:137–148), "Physiognomy of vegetation, formations, associations, varieties of associations," insists, with no substantial evidence, that physiognomy (landscape appearance) is of scientific interest and is determined by seven characteristics: dominant growth forms, density, height, and color of vegetation, seasonal relationships, duration of species life, and number of species. The term "formation" had been introduced by Grisebach (1838), but had come to mean for Warming (1909:140), "a community of species, all belonging to definite growth-forms which have become associated together by definite external (edaphic or climatic) characters of

the habitat…" If that seems a bit vague, his six examples of formations are not: microphyte, moss, herb, dwarf-shrub and undershrub, bush-wood or shrub-wood, and forest. But then he discusses simple formations, compound formations, secondary formations, and sub-formations. Humboldt had introduced the term "plant association" in 1807. For Warming (1909:145), "An **association** is a community of *definite floristic composition* within a formation; it is, so to speak, *a floristic species of a formation which is an oecological genus*." An association may occur as patches in a formation or exhibit zonal arrangement. But there are also varieties of association, such as edaphic or geographical varieties.

Warming's book was quite influential (Cittadino 1990:147–148). It was a paradigm in Thomas Kuhn's sense (1970:42–51): a program of research for plant ecologists. However, Warming, no more than Kerner, became the Linnaeus of plant ecology. In 1900 Flahault addressed the continuing problem of descriptive terminology in his "Projet de nomenclature phytogéographique." He was unimpressed with Kerner's suggestion that all the terms needed could be named in German. Matagne (1998:435) thinks that

> *By proposing straightaway in his* Projet *in 1900 that nomenclature must apply to geographical and topographical as well as to biological units, Flahault situated the problem clearly within the framework of the ecological approach to the relationship between living beings and the environment.*

However, Flahault's system was not definitive either, and the Second International Botany Congress (1905) charged him and German-born Swiss botanist Carl (Joseph) Schröter (1855–1939) with heading a committee to establish terminology "that integrated the floristic and physiognomic components of botanical geography" (Matagne 1998:436) for the Third International Botany Congress (1910). Schröter had studied botany at the University of Zurich under Professor Oswald Heer (1809–1883), who also taught entomology. Schröter succeeded his mentor and was Professor of Botany at the University of Zurich from 1879 to 1925; he coined the terms "autecologie" (1896) and "synecologie" (1902), according to Chapman (1931:5–6). Furthermore, Schröter's *Planzenleben der Alpen* (1904–1908) "was the start of an understanding of relationships between the growth of high mountain plants and their patterned and severe environments" (Billings 1985:6). His book "contains most of the knowledge of the time on the influence of elevation, soil, climate, and other environmental factors on alpine plants and plant communities" (Gigon et al. 1981:314). At last, Europe had a worthy companion to Kerner's *Das Pflanzenleben der Danaulaender* (1863). However, Schröter's monograph has 1288 pages, and no one has translated it into English. Although the 1910 Congress did not fully accept Schröter and Flahault's proposals, in 1913 their proposal provided the basis for the Zurich-Montpellier school of phytosociology (Becking 1957:426–463, Shimwell 1971:45–47, Lévêque 2003:18–19). Yet their methods "were not applicable everywhere, especially in Scandinavia, with its limited flora" (Becking 1957:419–426, Matagne 1998:437). Therefore, other regional schools formed, and a uniformity of concepts and methods became an elusive dream.

Josias Braun-Blanquet (1884–1980), Swiss, was a student of both Flahault and Schröter, and he became Flahault's successor at Montpellier (Nicholson 1989:142–143, 146–148, 181). His important influence came from publication of his *Pflanzensociology* (1928), which is beyond the scope of this part 48 survey, but he had begun publishing his version of phytosociology in 1913.

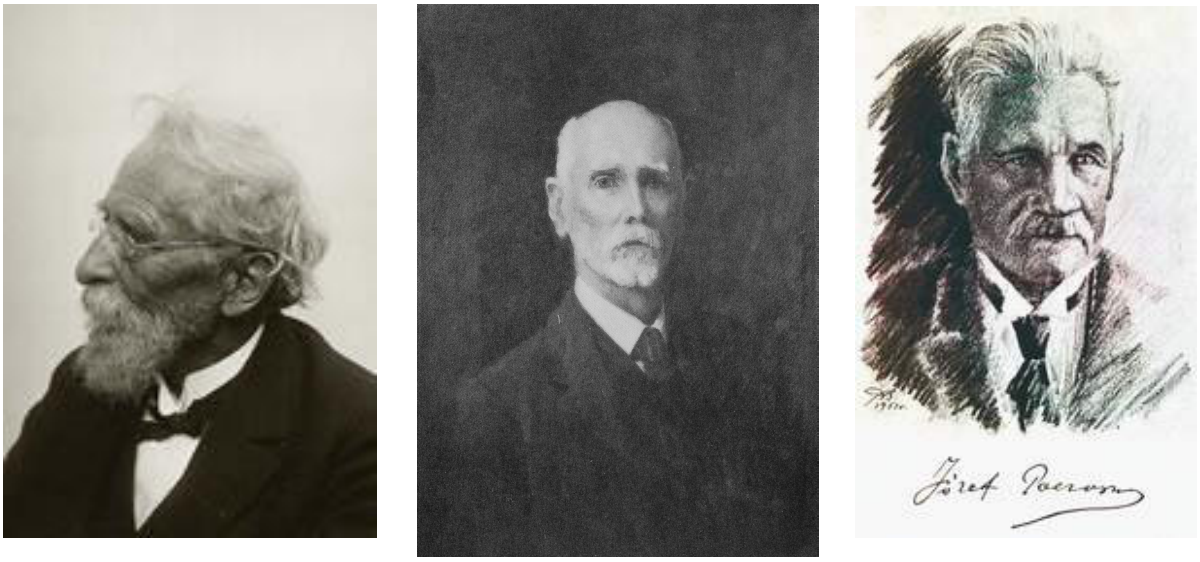


Fig.4. (a) Carl J. Schröter. Web site. (b) Leonard Cockayne. Thomson 1983.
(c) Józef Paczoski. Web site.

Three modern plant ecologists responded to this awkward nomenclature-classification situation by explaining the different systems and seeking some common understanding. A Dutch plant ecologist working in the United States, Rudy Becking (1957), explained the Zurich-Montpellier system to Americans, but found he also needed to explain competing systems. Robert H. Whittaker, at Brooklyn College, took a similar approach, with more details, in his "Classification of Natural Communities" (1966, 1977). English phytogeographer David W. Shimwell thought it would help to go into even more detail than either Becking or Whittaker in his *Description and Classification of Vegetation* (1971).

Phytogeography did not fade away with the growth of plant ecology. German systematic botanist H. G. Adolf Engler (1844–1930) collaborated with Drude in editing *Die Vegetation der Erde* (15 volumes, 1896–1923), to which Engler contributed volume 9: *Die Pflanzenwelt Afrikas* (1910–1915). Engler recruited other botanists to write volumes on parts of the world matching their expertise (Stafleu and Cowan 1976–1988, I:757–797, Stafleu 1978). An example of this recruitment was Leonard Cockayne (1855–1934), whom Engler recruited to write the volume on New Zealand (Hill 1935, Moore 1967, Thomson 1983). Cockayne was from Derbyshire, England, and he had attended Owen's College, Manchester, 1872–1874, then immigrated to Australia in 1876 and taught school there until 1880, when he went to New Zealand, where he continued teaching for four or five years. Afterwards, he bought land for farming and gardening. In 1877, he obtained a book on New Zealand ferns by G. M. Thomson, which turned his attention to native plants. He decided to devote his life to gardening and New Zealand botany.

"The Cockayne period in New Zealand botany may be said to have begun in 1896 when Diels of Berlin published his 100-page account of *Vegetations-Biologie von Neu-Seeland*" (Moore 1967:3). Diels had

not been to New Zealand (!) and depended upon accounts which Cockayne sent him. Diel's publication aroused the interest of Prof. Karl Ritter von Gobel, Munich University, who visited New Zealand in 1898, and Cockayne took him around the country, showing him the plants and their environments. This expedition of several weeks was mutually beneficial, and in 1903 Gobel had his university confer upon Cockayne an honorary Ph.D. For his part, Gobel conveyed to Cockayne the ecological perspective that was developing in Europe, and Cockayne read Warming's text, in German (Star 2006:198).

In 1890 there was an extensive fire in a subalpine beech forest near Arthur's Pass (930 m). In 1898 Cockayne published "On the burning and reproduction of subalpine scrub and its associated plants with special reference to Arthur's Pass District." That study initiated "the longest recorded and best documented example of plant succession in [New Zealand's] ecological literature" (Mark 1981:424). He also published on an ecological experiment in 1898, and in 1900 he published "A sketch of the plant geography of the Waimakariri River Basin, considered chiefly from an Oecological Point of View." He published a series of ecological surveys, then synthesized them into *New Zealand Plants and Their Story* (1910, edition 3, 1927). However, his earlier papers and Gobel's conferring of an honorary degree on him attracted Engler's attention, and he asked Cockayne to write the New Zealand volume of *Die Vegetation der Erde*. Cockayne was thrilled and reported to a friend in May, 1904: "Of course it is a most high honour for a colonial botanist to be invited to contribute towards such a series, where every work is supposed to be of the highest excellence…" (quoted in Moore 1967:5). He sent in his manuscript in 1914 to Leipzig, and then worried throughout World War I whether it would ever be published. After the dust and ashes of war had settled, *The Vegetation of New Zealand* appeared (Cockayne 1921, 364 pages, edition 2, 1928, 456 pages). Cockayne used his ecological knowledge to persuade New Zealand's government to establish or enlarge national parks (Star 2006:198). Besides his books, Cockayne published 184 articles, 40 being on ecology and 25 on plant distributions (Thomson 1982,1983:15–17). In 1932, he and J. D. Calder published "The Present Vegetation of Arthur's Pass (New Zealand) as Compared with that of Thirty-Four Years Ago."

Another example of Engler's recruitment was of John Harshberger to write the North American volume (see below). The 15 volumes that Engler and Drude edited was a monumental climax for a century of phytogeography, which began with Humboldt.

Phytosociology arose in the 1890s from the work of Jozef Konradovich Paczoski (or Pachoskii 1864–1942), born in Bialograd, southwestern Ukraine to Polish parents (Maycock 1967:1031, Kajak and Pieczyska 1981:287, Kozlowski and Sevedrzyuski 2009). He attended the School of Agriculture and Horticulture in Human, then the University of Kiev, 1888–1894. He was assistant curator of the Botanical Garden, Leningrad, 1894–1895, assistant in the School of Agriculture in Dublany, 1895–1897, director of the Natural History Museum in Cherson, 1897–1920, director of Steppe Reserve at Ascania Nova, 1922–1923, director of the National Park of Bialowieza, Poland, 1923–1928, and professor of plant systematics, sociology and geography at University of Poznan, 1925–1931, where he founded the first Institute of Plant Sociology.

Paczoski's first published paper was floristic, "Essay on the Flora in the vicinity of Umani, Gubernia of Kiev" (in Russian, 1887). In 1898, he persuaded a landowner to enclose 500 hectares of virgin steppe

on his estate, Askania-Nova, at the mouth of the Dnnepr River, for scientific research (Weiner 1988:16, 22). Beginning in 1891, he published studies in plant taxonomy and geography, while also developing his ideas on phytosociology, "Stages in the development of vegetation" (in Polish), and continuing in "The social life of plants" (1896, in Polish). Paul Maycock summarized the latter paper (1967:1033):

> *...which includes a definition of plant sociability, exclusion due to competition, simple and complex communities, the mutual exclusion principle, plant succession at the autecological level, root layering and competition, seasonal competition and aspection in steppe communities, dominance and subdominance, characteristics of community boundaries, community complexity and variability, influence of vegetation on soils, soil moisture and microclimate, shade tolerance, tolerance ratings of forest trees, tree reproduction and forest succession as related to tolerance, protophilous and sciophilous species, mutual intolerance, fire succession, the organismic concept, the plant formation and lower phytosocial groupings, actual and climatic limits of a species, restriction of ecological amplitude due to competition, etc.*

In 1921, Paczoski synthesized his studies in *The Principles of Phytosociology* (346 pages, in Russian), and applied these principles in his "Phytosociology and Forestry" (1925, in Polish). A controversial aspect of his concept was drawing an analogy between plant and human societies (Weiner 1988:65). He continued publishing until 1935, and his last two publications appeared posthumously after World War II (Maycock 1967:1034). His influence was not widespread.

A Russian botanist who knew Paczoski and his work, P. N. Krylov, published "A Synopsis of the Vegetation of Gubernia of Tomsk" (in Russian, 1898) without acknowledging Paczoski's work (Maycock 1967:1032). The work of Paczoski, Krylov, and other Russian phytosociologists of the 1890s "culminated in the full-blown forest system of Georgii Fedorovich Morozov of 1904, shedding Linnaeus's mechanism for an exuberant organicism that was mirrored in the work of an American, Frederic Clements, published the same year," as indicated in this Morozov passage about a forest community (quoted in Weiner 1988:64):

> *...not a mechanistic aggregation of trees, but a complex organism, all parts of which condition each other, and which lives its own life.... We must study these complex organisms as we study any organism: from the perspective of its morphology, properties, origin, transformations over the course of its lifetime, reproduction or regeneration, etc.*

Apparently, the studies of Paczoski, Krylov, and Morozov attracted no attention in Western Europe, as the English biogeographer David Shimwell mentioned none of them in his historical survey, *The Description and Classification of Vegetation* (1971). Shimwell also overlooked Maycock's article on Paczoski (1967), in *Ecology*.

Animal ecologist Daniil Nikolaevich Kashkarov (1878–1941), who first offered university courses in ecology in the Soviet Union, taught at the Middle Asian University, Tashkent, 1919–1933, then at the Leningrad State University, 1934–1941. He obtained a Rockefeller Foundation Fellowship for study in America, and afterwards he founded the *Journal of Ecology and Biocenology* (in Russian) (Josephson et al. 2013:107).

RUTGER SERNANDER
Målning av E Österman
Foto Bergianska stiftelsen

Fig. 5. (a) Aimo Kaario Cajander. Web site. (b) Rutger Sernander. Web site. (c) Lars-Gunnar Romell. By Gunnar Bruseqitz. Söderqvist 1986: cover.

At a practical level, foresters were interested in assessing the quality of different forest sites. Two Russians who studied the question focused on differences in ground cover. I. I. Gutorovich (1897) explained the logic of this approach, and G. F. Morosov (1904) "brought such information together in a classic paper which set up a classification of northern forests based on the use of ground cover plants and reproductive capacity of the trees as important indicators of soil conditions and, thus, of forest site quality" (Billings 1985:6). If Finish botanist Aimo Kaario Cajander (1879–1943) read Russian, he presumably would have read their studies. Nevertheless, circumstances steered him in the same direction. In a generation after Hult, he studied at the University of Helsinki under plant sociologist Johan P. Norrlin (1842–1917) and investigated vegetation along the Finnish–Russian border (Collander 1965:78–80). Cajander's great botanical work was *Kenntnis der Vegetation der Alluvionen der nördlichen Eurasiens* (three parts, 1903–1909). After publishing two parts of it, he accepted a government request that he head and reform Finland's forestry education system (Collander 1965:80). In "Ueber Waldtypen" (1909), he explained that "growth of trees of a given species was quite different depending upon forest type, as defined by ground cover, but varied relatively little *within* a single forest type, as so defined. This is an early and practical union of phytosociology and physiological ecology" (Billings 1985:6). Cajander was prime minister of Finland in 1922, 1924, 1937–1939 (Ilvessalo 1965:119–120).

A Swedish plant ecologist, Hugo Sjörs, published a brief history of Swedish ecology (1981), much of which he had lived through since the 1930s. It has few similarities to a detailed account which historian–sociologist Thomas Söderqvist published (1986). Söderqvist's main interest was in the growth of the ecological community rather than in what that community accomplished. There is a hint of that perspective in his title: *The Ecologists: from Merry Naturalists to Saviours of the Nation*, which is spelled out more precisely in a subtitle: *A Sociologically Informed Narrative Survey of the Ecologization of Sweden,1895–1975*.

(Johan) Rutger Sernander (1866–1944) was a phytogeographer at the University of Uppsala influenced by Hult (mentioned above) who trained several plant ecologists. He followed in Linnaeus' footsteps (1741, 1973) in studying the vegetation of Gotland Island (for his doctoral dissertation, 1894). In 1895 he was appointed docent of phytogeography at Uppsala, and in 1908 as professor of plant ecology (Fries 1950:70–71, Söderqvist 1986:46–47). In 1908–1910, his seminar ran a survey of Swedish vegetation comparable to the one that Tansley ran in Britain (Söderqvist 1986:54; on Tansley, see below). One of Sernander's very promising students was Thore C. E. Fries (1886–1930), son and grandson of Uppsala professors of botany (Söderqvist 1986:88–89). Fries studied "synekologie," on the relationship between climate and vegetation. He thought plant communities were natural units which could be revealed by induction. Gunnar Samuelsson (1884–1944) also studied at Uppsala and claimed that Fries' plant communities were "artificial groupings." "As a result of these prolonged seminar discussions the principles and methods of what later would be known as the Uppsala school emerged" (Söderqvist 1986:89). This school emphasized "that an association can be characterized by the occurrence of a group of so-called constant species," and this school gave up Fries' synecology in favor of a science of plant sociology (Söderqvist 1986:90). Fries then left ecology for systematics. Leading the way in plant sociology was another Sernander student, G. Einar Du Rietz, who published *Zur methodologischen Grundlage der modern Pflanzensoziologie* (Vienna, 1921). However, we saw above, that Jozef Paczoski had begun developing phytosociology in the 1890s and that he had also published in 1921 *The Principles*

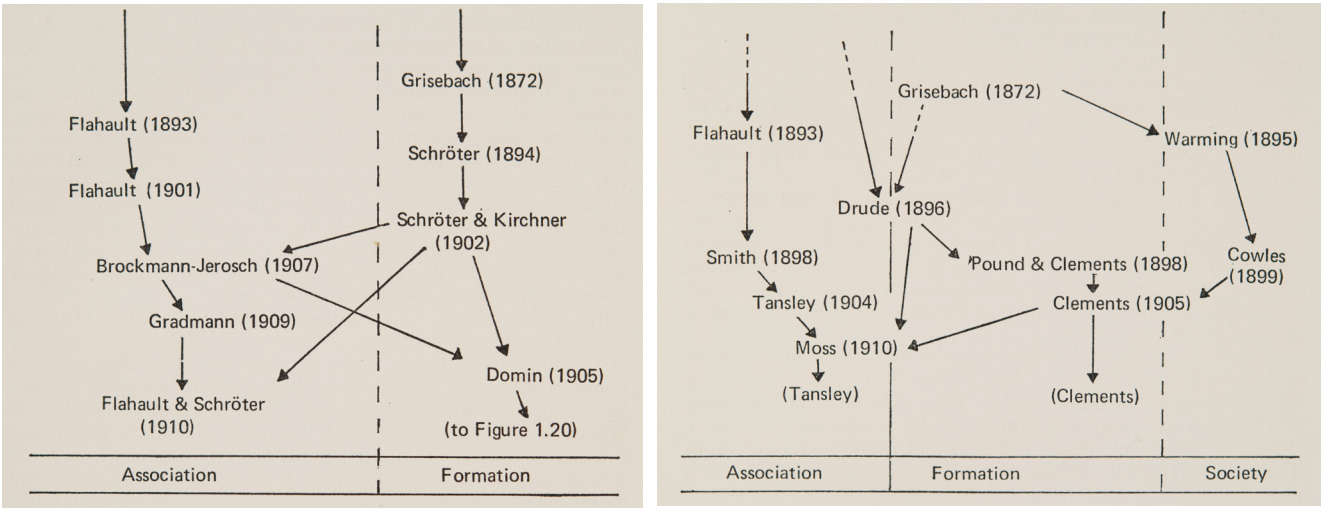


Fig. 6. (a) Origins of Zurich-Montpellier Tradition. (b) Origins of English Tradition. Two of six charts with which Shimwell (1971:46–47) illustrated evolving concepts which plant ecologists developed for understanding vegetation.

of Phytosociology in Russian. Du Rietz founded a plant sociology society in 1921 and a journal in 1929 (Söderqvist 1986:90).

In contrast to Sernander's phytogeographical emphasis at Uppsala, Henrik Hesselman (1874–1943) at the University of Stockholm followed the Germanic example of laboratory studies relating to ecology (Söderqvist 1986:56–58). Hesselman had his undergraduate degree from Uppsala, but in graduate school, he studied under Stockholm plant geographer Gunnar Andersson. In 1906, Hesselman became botanist for the Forestry Institute, founded in 1902, and editor by 1907 of the forestry journal *Skogsvårdsföreningens Tidskrift*. "Sernander's and Hesselman's local departments would turn out as the main centers for ecological research during the following decades" (Söderqvist 1986:58). Two of Hesselman's students stood out: Henrik Lundegårdh (1888–1969) and Lars-Gunnar Romell (1891–1981). Lundegårdh followed Hesselman into ecophysiology, and private donors funded for him Sweden's first field station on the island Hallands Väderö (Söderqvist 1986:96–99). Lundergårdh believed he could combine plant geography with experimental physiology. He published the first ecology textbook in Swedish, *Klima und Boden* (1925), which was praised in Germany and attacked in Uppsala. Lundegårdh accused Du Rietz of barren classification studies, and the latter accused Lundegårdh of being speculative and careless and not knowing the names of plants he studied (Söderqvist 1986:106–107).

However, it was ecophysiologist Romell who pursued the "Great Polemic" against Du Rietz and his Uppsala followers (Söderqvist 1986:108–115). Romell did not even make common cause with Lundegårdh, accusing him of being fixated on apparatus. Romell thought plant sociology could attain some value if it combined with ecophysiology, but that Du Rietz only did field descriptions using a quadrat. Du Rietz responded that Romell's ecophysiology was a vicious circle. The descriptive–empirical ideal prevailed at Uppsala and the hypothetical–experimental ideal at Stockholm. When the botany chair

at Uppsala became vacant in 1933, Du Rietz, Lundegårdh, and Romell all applied for it. When it went to Du Rietz, the Great Polemic ended. Lundegårdh turned to physiology and biochemistry, and Romell traveled to Cornell University for a year.

Hewett Watson (1804–1881) published on British plant geography for four decades, but he had no disciple to continue his work (Egerton 1979, 2003), and later botanists found inspiration abroad. Plant ecology arose in Britain as a result of the influence of publications by Warming, Schimper, and Flahault (Tansley 1947, Godwin 1977:4, 9).

Francis (Frank) Wall Oliver (1864–1951) was the son of a botanist who taught at University College, London (UCL) and became one himself (Salisbury 1952, Desmond 1977:472). In summer 1885 he studied in Bonn and became friends with Schimper, who interested him in ecology (Ayres 2012:65–66). Oliver's article for the Royal Horticultural Society "On the effects of urban fog upon cultivated plants" (1891) in London may have been the earliest scientific study of the effects of what we now call "smog." As far as remedies were concerned, he cautiously pointed out that his study was preliminary, and more data should be collected by others (Oliver 1891:149). Since his study dealt only with cultivated plants, his suggestion to grow them only in greenhouses that did not admit the "fog" was sensible advice. Only when studies on the effects of smog on Londoners after World War II would it become possible to legislate against air pollution.

Arthur G(eorge) Tansley (1871–1955), also from London, attended University College London (UCL) for 18 months during 1889–1890 and studied under Oliver, who may have interested Tansley in ecology. However, by then Tansley was already committed to botany. At age 12 he had written in his school newspaper on two species of *Potentilla* (Ayres 2012:3). In 1890, Tansley transferred to the Botany School, Cambridge University, where he and a close friend, philosopher Bertrand Russell, founded a university newspaper, which they ran for 21 issues (Ayres 2012:45). Tansley graduated with honors in 1894 (Godwin 1977:2–19, Ayres 2012:48), then returned to teach at UCL until 1907, when he returned to Cambridge University. At UCL, he assisted Oliver in translating and revising Kerner's *Pflanzenleben* (1890–1891),which was published as *The Natural History of Plants: Their Forms, Growth, Reproduction, and Distribution* (1896). In 1898, Tansley studied the German edition of Warming's book and compared English plant communities with those Warming had described in Denmark. He also taught a course based on that book in 1899. (Later, he found the 1909 English version of Warming's book less satisfactory than the 1896 German version [Tansley 1947:130].) In July 1903, Oliver led UCL students and staff on a field trip to the East Norfolk Broads, and in summers, 1904–1907, he took UCL students for a two-week trip to northern France, which set an example for Tansley (Tansley 1947:133, Ayres 2012:65). UCL was the first British university to admit women students, in 1878. Edith Chick entered UCL in 1889 and graduated with honors in botany in 1894, the same year that Tansley graduated from Cambridge. They married on 30 July 1903. In 1902, Tansley used his own money to found a new journal, *The New Phytologist* (Ayres 2012:71), the name suggested by Oliver. (*The Phytologist* was a London journal, 1840s–1860s, which Watson dominated, though he was not its editor.) Tansley edited *The New Phytologist* for thirty years, and it continues to flourish. In its first volume he suggested that full-time botanists could coordinate surveys made by local botanical or natural history clubs (Lowe 1976:528). After Britons had published several vegetation surveys, Tansley suggested in a commentary

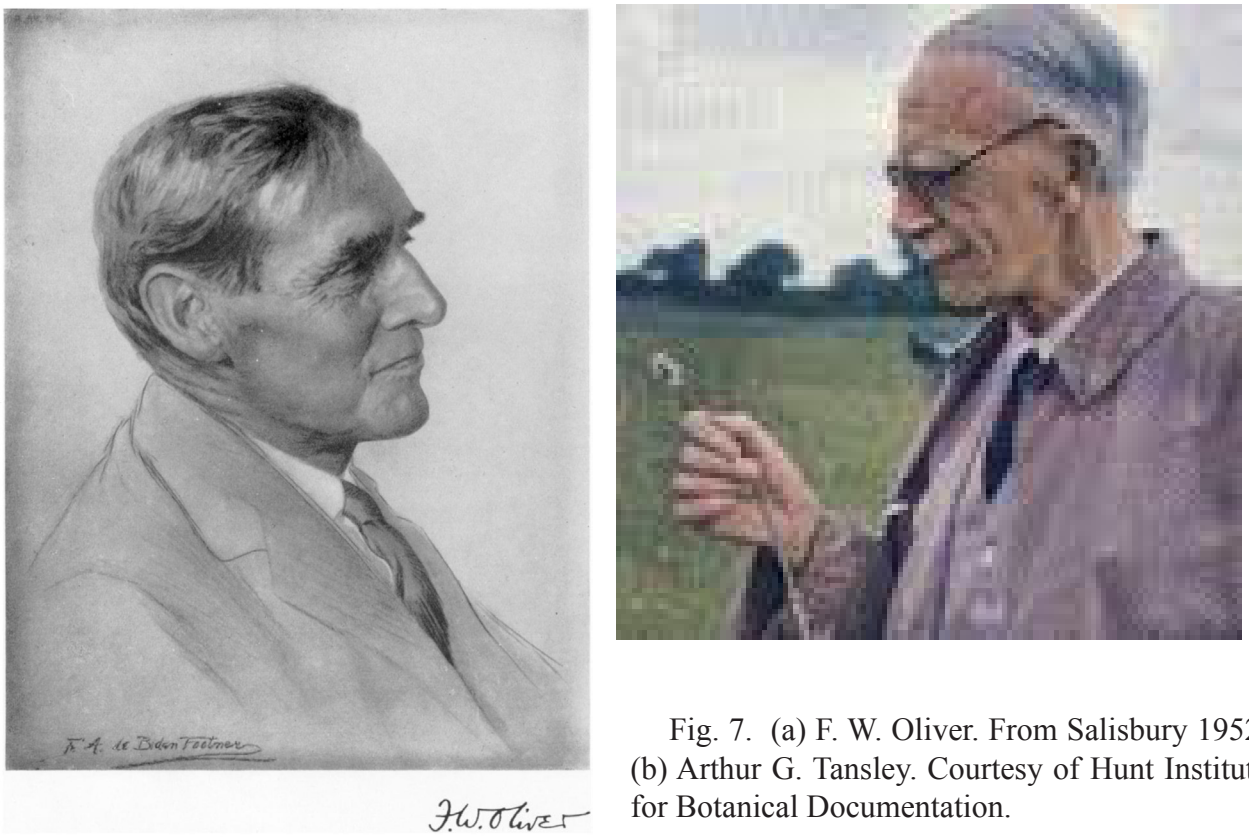


Fig. 7. (a) F. W. Oliver. From Salisbury 1952. (b) Arthur G. Tansley. Courtesy of Hunt Institute for Botanical Documentation.

on "The Problems of Ecology" (1904) that authors of surveys form a British Vegetation Committee to achieve uniformity of methodology and to compare their findings (Sheail 1987:22–29, Ayres 2012:70). They did, and Tansley, of course, ran the committee, which, in 1905 published a six-page pamphlet, *Suggestions for Beginning Survey Work on Vegetation*.

At Cambridge, Tansley had met fellow Londoners and botany students, Vernon and Frederick (Fritz) Blackman. In 1905, after the American plant ecologist Frederic E. Clements published *Research Methods in Ecology*, Fritz Blackman and Tansley published a 27-page review of it in *The New Phytologist*. Why such a long review? "Dr. Clements' book is at once the most ambitious and most important general work on Ecology that has been published during the last seven years" (Blackman and Tansley 1905:199). They shared Clements' impatience with those who "did ecology" without training, and they shared his belief that ecology is "the central and vital part of botany" (Blackman and Tansley 1905:201). However, an entirely laudatory review would not require 27 pages. What Tansley encountered in Clements' *Research Methods* were insights worthy of detailed discussion, generating many arguments along the way. In a letter written on January 12, 1906, Clements thanked the reviewers for their "fair, critical and yet appreciative review in the *New Phytologist*" (Tansley Archives at Cambridge University, quoted from Ayres 2012:69).

Charles Edward Moss (1870–1930) was a member of the British Vegetation Committee who developed

a three-level hierarchy of vegetation units, with "plant formation" being the largest, for uniform habitats, "plant association" being for areas of variation within formations, and "plant society" being the smallest units within associations; but at the International Botanical Congress (1910), Flauhalt and Schröter rejected Moss' scheme as unsuitable for Continental Europe (Ayres 2012:75–76).

There was an International Congress of Geography held at Geneva in 1908, for which Schröter organized a national tour of Swiss types of vegetation (Fischedick and Shinn 1993:110). Tansley was (1947:134)

> *...much impressed by the benefits of the contacts made and the amount that could be learned from the examination of vegetation under the guidance of native botanists who had studied it, besides the stimulative effects of the comments of foreign visitors: and on my return to England I suggested to the Committee that we should try to organize a similar international excursion in the British Isles.*

The findings of the British Vegetation Committee appeared in *Types of British Vegetation* (1911), which Tansley edited and mostly wrote. *Types* also served as an introduction for the very successful International Phytogeographical Excursion in Britain which Tansley organized and ran (Sheail 1987:30–35, Fischedick and Shinn 1993:110–111, Cameron and Matless 2011; Ayres 2012:83–87 includes a map of the route). Americans participating were Clements and Cowles and their wives (Golley 1993:14).

The Vegetation Committee having achieved its objective of describing British vegetation, Tansley led its transformation into the British Ecological Society in 1913—the world's first such society—and animal ecologists were invited to join (Pearsall 1964:1–2, Duff and Lowe 1981:141–144, Sheail 1987:36–44, Fischedick 2000, Ayres 2012). Tansley was its first president (and the only president serving two years). He also initiated its *Journal of Ecology*, which was also a first, begun in 1913. Tansley became its editor in 1916, after relinquishing the presidency. (Oliver became the second president.) It was primarily a plant ecology journal. Despite Tansley's incisive mind and intellect, he accepted American plant ecologists Clements and Cowles as equals, learning from them, and crediting them for their achievements. In 1923, Tansley published *Practical Plant Ecology: A Guide for Beginners in Field Study of Plant Communities for British Students*. By today's standards, it is rather brief for a college or university textbook, and he did not specify whether he expected students at that level or lower levels to use it. It remains of interest as indicating his perspective on the scope of plant ecology in 1923, and it was published in New York as well as in London.

Drude published *Die Ökologie der Pflanzen* (1913), the first plant ecology textbook. Warming's *Plantesamfund* (1895), with subsequent translations into German and English, had served as a textbook in the absence of one. Arthur Tansley (1914) gave Drude's text a 2.5-page review in the *Journal of Ecology*. The tone of his review is neutral, and he merely summarized the book's contents. His only negative comment was that "The price is, perhaps, rather high." Yet when Tansley published his own *Practical Plant Ecology*, he stated (1923:7):

> *There are, so far as my knowledge goes, only two books in existence which have at all the same objects as this—Dr. Clements's* Research Methods in Ecology *(1905) and Dr. Rübel's* Geobotanische Untersuchungsmethoden *(1922).*

It is unlikely that Tansley deliberately snubbed Drude's book in this statement—a tactic uncharacteristic of Tansley—he had simply forgotten a book he had reviewed a decade earlier that had not impressed him at the time.

North America

Americans responded to the emergence of a new science of plant ecology at about the same time as the British, and, like Britain, mostly in response to European literature (Gleason 1975, Kohler 2002:74–77). Plant ecology grew more rapidly in North America than in Europe because the American system of higher education was still expanding during the early 1900s, and so it was easier to add faculty in new specializations in America than in Europe. Furthermore, American universities did not copy the European tradition of having only one professor in a department. Two professors of botany who first trained plant ecologists were Bessey from Ohio and Coulter from Indiana (Egerton 1976:340–341, 350, McIntosh 1976:353–354). Charles Edwin Bessey (1845–1915) earned B.S. and M.S. degrees from Michigan Agricultural College, taught at Iowa Agricultural College, which awarded him a Ph.D., and in 1884 became Professor of Botany at the University of Nebraska (Ewan 1970, Tobey 1976, 1977, 1981:9–45, Cittadino 1980:175–178, Ewan and Ewan 1981:18, Overfield 1993, Isely 1994:237–240, Burgess 1996:14–15), where he trained ecology students Conway MacMillan, Roscoe Pound, and Frederic E. Clements. John Merle Coulter (1851–1928) was botanist to F. V. Hayden's geological survey of the Yellowstone region in 1872 and later collaborated in writing floras of Colorado and Indiana (Rodgers 1944, Stafleu and Cowan 1976–1988, I:558–559, Ewan and Ewan 1981:49–50, Tobey 1981:124–126, Cittadino 1993:527–531, Isely 1994:251–253, Burgess 1996:31). He earned a Ph.D. from the University of Indiana in 1884 and became Professor of Botany at the University of Chicago in 1896. He trained ecologist Henry Chandler Cowles, who remained at that university and in turn trained other plant ecologists.

Bessey's student, Conway MacMillan (1867–1929), from Michigan, received bachelor and master's degrees from the University of Nebraska in 1885 and 1886, studied further at Harvard and Johns Hopkins, then became instructor in botany (1887) and later professor at the University of Minnesota (Humphrey 1961:159–160, Egerton 1976:340, 350, Stafleu and Cowan 1976–1988, III:230–231, Cittadino 1980:184–186, Burgess 1996:70–71). His *Metaspermae of the Minnesota Valley* (1892) contains a capable ecological survey of the plants of the region, following the German tradition of Kerner, Drude, and other botanists. MacMillan continued publishing similar studies until 1897; his last one, "Observations on the Distribution of Plants along Shore at Lake of the Woods," at the Canadian border, being a project somewhat similar to the one Cowles began at about the same time along the shore of Lake Michigan. MacMillan headed Minnesota's Botany Department until 1906 and headed a state botanical survey, 1900–1906 (Kohler 2006:100), when he became dissatisfied with the modest salary of professors and left academia for business.

Roscoe Pound (1870–1964) was practically a bystander, who succumbed to the enthusiasm for the new botany (Wigdor 1974: chapter 3, White 1981, Burgess 1996:89). From Lincoln, Nebraska, a judge's son, and later dean of Harvard Law School, he spent the academic year 1889–1890 at Harvard Law School, then returned home to practice law with his father, while also enrolling at the University of Nebraska

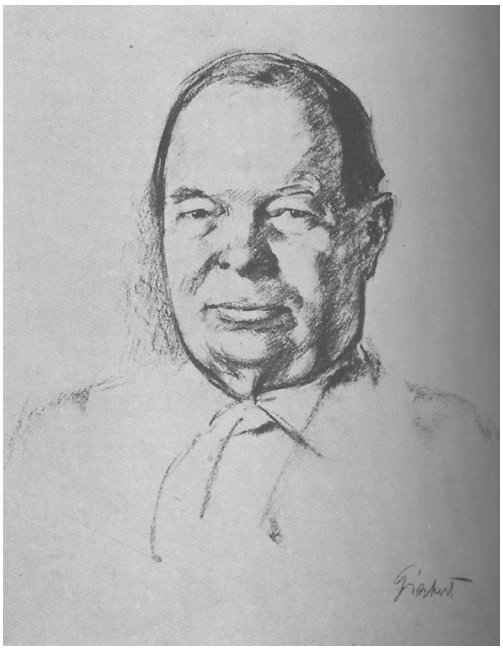


Fig.8. (a) Frederic E. Clements. *Ecology* 35:108.
(b) Henry C. Cowles. *Ecology* 16:281.

for a doctorate in botany. The "action" in botany centered on the student's "Sem[inar] Bot[any]," which focused on a survey of Nebraska's flora (Overfield 1993:132–138). Pound's "Symbiosis and mutualism" (1893), published two years before Warming's book discussed the subject, was first presented to that seminar. Sapp (1994:30–31) faults Pound for over-emphasizing struggle and discounting "mutualistic symbiosis." Pound headed the Botanical Survey of Nebraska, staffed by the seminar (Kohler 2006:104–105), and was senior author of *The Phytogeography of Nebraska*, which became a joint Ph.D. dissertation with Frederic E. Clements (1874–1945), then a publication (Pound and Clements 1898, edition 2, 1900). Pound received his Ph.D. in 1896; Clements waited until 1897, delayed by a language requirement.

Pound and Clements, with Bessey's assistance, adapted and modified Drude's methods for German vegetation to Nebraska's prairie (Tobey 1981:51–58, Nicolson 1989, Overfield 1993:148–149). They found that the most prominent species were not always the most abundant (Tobey 1981:66), so they wanted an objective methodology, which they perfected during the spring and summer of 1897 and subsequently published (Pound and Clements 1898). They used a quadrat to sample an environment, counting the individuals of each species within the square (Tobey 1981: chapter 3, Kohler 2002:100–105).

A balanced review of their *Phytogeography* (Cowles 1898, 2007) asserted that it was an indispensable work for American ecologists, but complained about their terminology that "used Greek derivatives in place of the simpler and more expressive English equivalents." Since science goes beyond everyday experience, and therefore needs new terminology, this complaint may seem simplistic. However, it was a persistent complaint against Clements, who tended to go beyond common sense, and it is interesting to see that this complaint started as soon as he began publishing.

Pound then followed his legal destiny to fame, and Clements became "the most influential [American plant?] ecologist of the first half of the twentieth century" (Tansley 1947, Clements 1960, Ewan 1971:317, Sears 1973, Stafleu and Cowan 1976–1988, I:510–511, Worster 1977:208–220, Ewan and Ewan 1981:43–44, Tobey 1981:76–87, Hagen 1988, 1999, Croker 1991:66–69, Hagen 1992:20–28, Isely 1994:326–330, Burgess 1996:26–27). Clements, like Pound, was from Lincoln, and he received B.Sc., M.A., and Ph.D. degrees from the University of Nebraska. He was a member of its faculty, 1894–1906, during which time he acquired a wife, assistant, and secretary in Edith Gertrude Schwartz (1877–1971). She received a doctorate in botany at the University of Nebraska in 1904 (Ewan and Ewan 1981:43, Tobey 1981:76–77, Burgess 1996:26). In 1907, Clements replaced MacMillan at the University of Minnesota, staying a decade before accepting his final employment as research ecologist at the Carnegie Institution of Washington. On their honeymoon, summer 1899, the Clementses visited Pikes Peak, Colorado and decided to establish an Alpine Laboratory at Minnehaha, near the cog railroad from Manitou Springs to the top of Pike's Peak. For three summers they collected plants and sold specimens to herbaria to pay for their laboratory, and thereafter spent summers there (Clements 1960:16–22). The Universities of New Mexico and Montana also established biological stations in 1899 (Vetter 2010:112). Frederic Clements dominated ecology largely because he worked hard and produced numerous publications. *The Development and Structure of Vegetation* (1904), *Research Methods in Ecology* (1905), and *Plant Physiology and Ecology* (1907) drew heavily upon methods and concepts developed with Pound, but were enriched by his further work while on the Nebraska faculty (Clements' bibliography: Pool 1954:110–112). These last three books plus the Pound and Clements volume established Clements as a prominent leader of American plant ecology and impressed Tansley in Britain (Tansley 1946).

In February 1913 Clements published in *Science* what today could be called an "infomercial," to attract graduate students to his Alpine Laboratory. (Bessey in 1895 had published news of a past summer school.) He explained that it was situated at 8500 feet elevation, on the Cog Railway between Manitou and the summit of Pike's Peak, and provided convenient access to "a unique series of great formational zones," which he briefly identified (Clements1913:327):

> *From the Great Plains grasslands, the series runs from valley woodland at 5,800 feet to mesa, chaparral, foothill woodland, pine forest, aspen woodland and spruce forest to alpine meadow, rock field and bog at 11,000–14,000 feet in a distance of 7 miles.*

He listed eight plant ecology publications (all his), 1904–1913, which drew upon data collected at this laboratory.

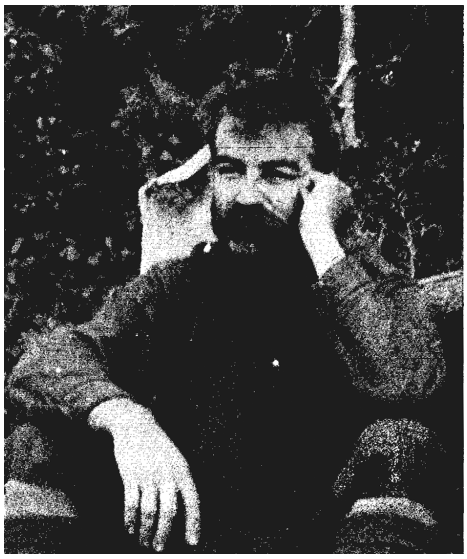
Meanwhile, Henry Chandler Cowles (1869–1939), son of a Connecticut market gardener, attended

Oberlin College, 1889–1893, where he studied botany and geology, and was president of both the botany club and Agassiz Association and graduated with high honors. He taught sciences at Gates College, Nebraska, for a school year (1894–1895), then spent the rest of his career at the University of Chicago (Sears 1958, Worster 1977:206–208, Ewan and Ewan 1981:50–51, Tobey 1981:104–108, Engel 1983:137–150, Mitman 1992:16–19, Cittadino 1993, Isely 1994:306–307, Burgess 1996:31–32, Cassidy 2007:5–29). When he arrived at Chicago in 1895, he was attracted to the courses of two geology professors, but in 1896, Coulter came to the University of Chicago as head of the Botany Department and Cowles decided to major in botany. Coulter taught an ecology course in spring 1896. Coulter was also founder and editor of *Botanical Gazette,* and when a review copy of Warming's *Lehrbuch der ökologischen Pflanzengeographie* (German edition, 1896) arrived, Cowles wrote a synopsis of if for Coulter, who reviewed it in *Botanical Review*. (Cowles reviewed books in practically every issue of *Botanical Review*, 1896–1933.) Warming's book had the same strong impact on Cowles that Drude's had on Pound and Clements, and in the same year! Coulter had published a paper on the flora of northern Indiana and took Cowles to the glaciated dunes along Lake Michigan—the largest dunes in the world. He apparently suggested that Cowles study their vegetation for his dissertation (Cassidy 2007:33). In the article based upon his dissertation, Cowles acknowledges (1899:97–98)

> *...his great indebtedness to Dr. Eugen Warming, professor of botany at Copenhagen: his textbook on ecology and his treatises on the sand-dune floras of Denmark have helped greatly to make clear the true content of ecology, and they have been a constant incentive to more careful and thorough work.*

There followed two articles which represented additional research beyond the dunes. It was a subject that drew upon Cowles' geological as well as his botanical knowledge, and one of the articles which he published afterwards was on "The influence of underlying rocks on the character of the vegetation" (Cowles 1901*a*, 2007). As Clements explained in his summary history of succession studies (1916:26), Pound and he had discussed succession of Nebraska plant formations, but not in the depth that Cowles did, as Cowles could follow succession from the coast inward and see successive stages representing different ages of vegetation. In this connection, Cowles introduced the term "climax" into ecology (Drouin 2013:55).

In 1903, a plant physiologist called attention to progress in plant ecology (Spalding 1903), and the following year Cowles did likewise. Others have commented upon the introduction to Cowles' report in which he confessed that "the field of ecology is chaos" (Cowles 1904:879). However, what is impressive about his survey is the great number of studies on which he reported, though without citing the journals in which those reports appeared. (The University of Chicago Library obviously subscribed to numerous botanical periodicals.) Plant ecology was flourishing throughout Europe and America! In 1909, Cowles (page 395) thought that it was "essential that physiology and ecology break down the barrier erected for them in Madison in 1893, where it was declared that physiology is experimental and ecology observational. The ecologist must experiment," though Cowles seems not to have followed his own advice. His best summation of his own studies was his presidential address at a meeting of the Association of American Geographers in 1910, "The Causes of Vegetative Cycles," which included a brief historical survey of pertinent ideas. He concluded (Cowles 1911:182, 1977)



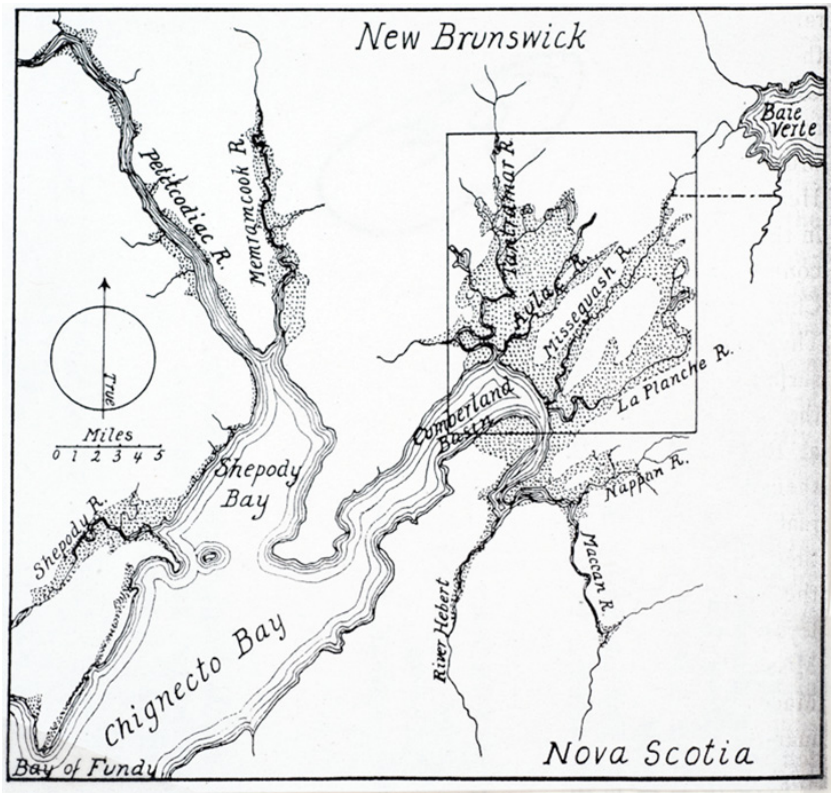


Fig. 9. (a) William F. Ganong. *Plant Physiology* 16 (1941) 215. (b) Locator map of study areas, which are dotted. The area in the quadrangle was enlarged in an adjacent map. Ganong 1903:164.

> *Each climatic cycle has its vegetative cycle; each erosive cycle within the climatic cycle in turn has its vegetative cycle; and biotic factors institute other cycles, quite independently of climatic or topographic change. It is small wonder that within this complex of cycle within cycle, each moving independently of the others and at times in different directions, dynamic plant geography has accomplished so little in unraveling the mysteries of succession.*

That is as far as Cowles himself was prepared to go, no doubt hoping his students would go further.

Clements, in his very large *Plant Succession: an Analysis of the Development of Vegetation* (1916), wrote the definitive American plant ecology work for that time, and for decades to come. In his review of this opus, Cowles acknowledged that "The work is thus a compendium of our knowledge and theories bearing on the phenomena of succession," but he lamented that Clements had "allowed his splendid classical training and love for Greek and Latin to carry him so far afield" (Cowles 1919, 2007). He also disagreed that succession is inevitably unidirectional to a climatic climax. Cowles' biographer commented that "Cowles was reviewing a study that he should have written himself" (Cassidy 2007:56). However, the division of labor between Clements and Cowles precisely fit their personalities and capacities. Clements was a solemn introvert with a great capacity to do solitary research and writing, while Cowles was a "people person" who easily assumed leadership roles in teaching, administration,

Fig. 10. (a) Daniel T. MacDougal. Web site. (b) Forrest Shreve. Bowers 1988:cover.

and in organizations. Each made the best uses of his talents: Clements produced numerous publications; Cowles produced very capable students and was active in several organizations. The enormous influence of Cowles' teaching is illustrated in a chart Douglas Sprugel constructed (1980). Cowles was, in 1918, third president of the Ecological Society of America (Burgess 1977:7). Because Clements had coauthors for some of his publications, a historian identified a Clementsian research school, then admitted "this success as an individual scientist [contrasts] with Clements's inability to create an effective research group" (Hagen 1993:193). However, instead of seeing a failed research group, one could see successful collaborations in publishing.

Other botanists, trained by neither Bessey nor Coulter and Cowles, nevertheless developed ecological interests during this formative period in America (Humphrey 1961, Cittadino 1980:187–194, 1997b, Nicolson 1990, Burgess 1996, Kingsland 2005, Egerton 2009*a*:56–72). One of them was Canadian William Francis Ganong (1864–1941), from St. John, New Brunswick (Bell and Whiteford 1979, Burgess 1996:45, Cittadino 1997*b*). He received B.A. (1884) and M.A. (1886) degrees from the University of New Brunswick in zoology, became interested in botany, and received a B.A. degree in it from Harvard (1887) and a Ph.D. in botany from the University of Munich (1894). For 38 years, Ganong was Professor of Botany at Smith College in Massachusetts, yet he returned every summer to St. John, where he studied marshes and bogs at the north end of Cumberland Basin along the boundary between

New Brunswick and Nova Scotia. Those waters eventually flow into the Bay of Fundy, which has the greatest tidal fluctuations in the world—over 40 feet in some places. He studied the plant associations along the water way and diagrammed their relationships in a very lengthy study (Ganong 1903, Egerton 1977*c*).

Frederick V. Coville (1867–1937), son of a prosperous farmer in New York State and graduate of Cornell University (Humphrey 1961:60–62, Stafleu and Cowan 1976–1988, I:561–562, Ewan and Ewan 1981:50, Burgess 1996:31). He became a botanist at the USDA and curator of the National Herbarium. Coville is most remembered ecologically for his explorations of Death Valley in 1891, recorded in his *Botany of the Death Valley Expedition* (1893).

Daniel Trembly MacDougal (1865–1958), from Indiana and graduate of DePauw University (1890), with a Ph.D. (1897) from Purdue University, researched on plant physiology (Moore et al. 1939, Stafleu and Cowan 1976–1988, III:216–217, Ewan and Ewan 1981:142, Bowers 1988:14–15, Kingsland 1991*a*:481–483, 1993:159–162, Isley 1994:299–302, Burgess 1996:70, Craig 2005:1–2, 8, 18–24, 37–53). He worked as research assistant at the New York Botanical Garden, 1899–1906. However, in 1903 he collaborated with Coville in selecting a site for a Desert Botanical Laboratory, on a small mountain, Tumamor, near Tucson, Arizona, founded by the Carnegie Institution of Washington (Coville and MacDougal 1903, McGinnies 1981:1–6). In 1906 MacDougal became its head and emphasized relationships between physiology and ecology (Billings 1985:14). In 1908 the Carnegie Institution opened a Carmel Laboratory on the California coast, which became summer headquarters for the Desert Laboratory (McGinnes 1981:11, Craig 2005:45–49).

MacDougal recruited a staff that included Maryland native Forrest Shreve (1878–1950), who had earned his B.A. degree (1901) and Ph.D. (1905) from Johns Hopkins University, with a dissertation on pitcher plants (Bowers 1988:4–7, Burgess 1996:99–100). In 1904, the Maryland Weather Service sponsored Shreve's field work to produce *The Plant Life of Maryland* (1910), which he mainly wrote, assisted by three other Maryland botanists (Bowers 1988:8–11). Clements by then had published his *Research Methods in Ecology* (1905) and *Plant Physiology and Ecology* (1907), which explained both his methods and concepts, but Shreve from the start resisted Clements' thinking and never changed his mind. *The Plant Life of Maryland* did not follow Clements' lead. While a graduate student in 1903, Shreve conducted research at the New York Botanical Garden's Blue Mountains research station in Jamaica, and in 1905 he returned for six months to study physiological ecology (Bowers 1988:11–13). He had not been trained in this field, and he used Schimper's *Plant-Geography upon a Physiological Basis* as a guide. In 1904–1905 Shreve taught at the Biological Laboratory at Cold Spring Harbor, Long Island and met MacDougal. In 1907 MacDougal decided to hire Shreve for research at the Desert Botanical Laboratory, with a provision that he complete his Jamaica research before undertaking desert ecology. His Jamaica experience proved valuable to Shreve for seeing the contrast between tropical rain forest ecology and desert ecology. Shreve arrived at the Desert Laboratory in June 1908 and devoted the rest of his career to desert plant ecology (bibliography in Bowers 1988:180–184).

Another example of the spread of research interest in ecology was botanist Thomas H. Macbride's establishment of a lakeside laboratory at Iowa's West Lake Okoboji in 1909 (Lannoo 2012:14–19). This lake is located in northern Iowa, near the Minnesota border (see "M" on map, Carlander et al. 1963:318),

and the laboratory continues to flourish after a century as a teaching and research field station for plant ecology, animal ecology, and limnology for students and faculty at the University of Iowa, Iowa State University, University of Northern Iowa, and other Iowa institutions of learning (Zieglowsky-Baker 1990, Lannoo 1996, 2012:49).

John W. C. Harshberger (1869–1929) lived all his life in Philadelphia and received B.S. and Ph.D. degrees in botany from the University of Pennsylvania (Harshberger 1929, Nichols 1930, Humphrey 1961:107–109, Stafleu and Cowan 1976–1988, II:59–60, Burgess 1996:52). He developed an interest in plant ecology without ever having studied it. Adolf Engler invited him to write what became Harshberger's *Phytogeographic Survey of North America* (1911, some 800 pages, 18 plates, and map), which is volume 13 of Engler and Drude's *Die Vegetation der Erde*. It was quite a feat for one botanist to synthesize all the floristic and vegetative literature for North and Central America and the West Indies, including changes from glacial times to recent times. Harshberger's *Survey* included "the first summary description of the major communities of North America" (McIntosh 1976:355). One obituary called the book "monumental" (Nichols 1930), but a knowledgeable systematic botanist called it "monumentally inaccurate" (Fernald 1911, 1926:511; on Fernald: Ewan 1971, Isely 1994:321–325). Harshberger did not respond in print to this humiliation, but later George Neville Jones published a ten-page reply to Fernald's fifteen-page trashing of his own *Flora of Illinois* (1945, Isely 1994:324). When Hafner reprinted Harshberger's *Survey* in 1958, the company may have known about Nichols' characterization, but it seems unlikely it knew of Fernald's. No subsequent botanist has been brave enough to top Harshberger's synthesis.

When Clements and Cowles participated in Tansley's four-week International

Fig. 11. John Harshberger. Web site.

Phytogeographical Excursion in August 1911, Cowles agreed to host a similar excursion in America, which he and Clements did in summer 1913 (Tansley 1913–1914, Nichols 1914, Fischedick and Shinn 1993, Cassidy 2007:51–52, 278–279, Beidleman 2009, Ayres 2012:87–90). It began in New York City in late July, with field trips to Long Island, New Jersey, and two botanical gardens, then off by train to Chicago, where Cowles showed the sites where he had described the changing vegetation. In Nebraska, Bessey met them while the thermometer reached 108° F in the shade. In southeast Colorado, Clements met the party and took them to Pike's Peak and his Alpine Botanical Laboratory. The Excursion proceeded to Salt Lake City, then to Mount Rainier, Washington, south to Oregon's Crater Lake, and into California's Siskiyou Mountains to Mount Shasta. In San Francisco on 7 September, Professor Willis Jepson became their host for visiting Yosemite National Park; Alice Eastwood

guided them into Muir Woods; then the excursion traveled to Carnegie Institution's Coastal Laboratory at Carmel, the Salton Sea surrounded by desert, and Carnegie Institution's Desert Laboratory in the Sonoran Desert; returning to New York in early October. Tansley, accompanied by his wife, Edith, was very impressed with the care taken for the excursion's success and with the continental panorama laid out before its members. He ended his very lengthy account of this American IPE with the comment (1913–1914:333): "In that vast field of ecology America has secured a commanding position."

In 1914, Clements became a research associate of the Carnegie Institution, and after publication of *Plant Succession*, MacDougal recruited him for his staff (Clements 1960, Bowers 1988:56–59). Not until 1918 did the Clementses buy a car; Edith became driver and did minor repairs (Clements 1960, Kohler 2006:178–179). Frederic and Edith Clements spent winters at the Desert Laboratory and summers at his Alpine Laboratory (Craig 2005:31–36). With a decline in Carnegie Institution annual endowment, its president, Vannevar Bush, decided to close the Desert Laboratory, which was transferred to the U. S. Forest Service in 1940, and to withdraw support for Clements' Alpine Laboratory (McGinnies 1981:15–16, McIntosh 1983, Craig 2005:85–91). In 1960, the Forest Service sold the Desert Laboratory to the University of Arizona for $140,500 (Bowers 1988:145), and it was headquarters for the prominent paleoecologist, Paul S. Martin (1928–2010) during 1957–2008 (Steadman 2011).

America's International Excursion may have provided a similar momentum for forming the Ecological Society of America (1915) that the British Excursion had provided for forming the British Ecological Society (Burgess 1977), though BES organizing was by botanists, while the first American suggestion for a society came from a zoologist. Professor of Zoology Robert H. Wolcott, at the University of Nebraska, wrote on 27 March 1914 to Instructor Victor E. Shelford at the University of Chicago, suggesting a regional organization (Burgess 1977:2, Croker 1991:120–121). Shelford discussed it with Cowles, who favored a national organization and arranged a planning session at the meeting of the American Association for the Advancement of Science on 30 December in a Philadelphia hotel, with at least 22 prospective members. They appointed a six-man organizing committee, and a year later, a group of about fifty met at the next AAAS meeting in Columbus, Ohio and formally organized the Ecological Society of America.

In 1916, ESA held its first summer meeting at San Diego, and on a field trip Clements and Illinoian Henry A(llan) Gleason (1882–1975) met and argued about plant communities (Nicolson 1990:111–112). Afterwards, Clements published his *Plant Succession* (1916) and Gleason published "The Development and Structure of the Plant Association" (1917). Gleason had his B.S. (1901) and M.S. (1904) degrees from the University of Illinois and his Ph.D. (1906) from Columbia University. He had previously published five ecological papers, but that was too slight an achievement compared to Clements' books to gain serious consideration of his critique from other plant ecologists (Gleason 1953, McIntosh 1975, Tobey 1981:170–171, Nicolson 1990, Hagen 1992:28–31, Isely 1994:334–39, Burgess 1996:46). However, there were also other skeptics. Michigan native Burton Edward Livingston (1875–1948) graduated from the University of Michigan, then at the University of Chicago studied plant physiology under Charles Reid Barnes and plant ecology under Cowles (Krikorian 1973, Kramer 1974, Burgess 1996:67). He spent 1906 at the Carnegie Desert Laboratory, where he and Shreve found common ground, which led to their *The Distribution of Vegetation in the United States as Related to Climatic Conditions* (Livingston and Shreve 1921), in which they "argued that no two plant species were quite identical in their habitat

requirements, and hence no two plants had identical patterns of distribution" (Nicolson 1990:137). Gleason was not at all discouraged by the scant notice his 1917 paper had received and subsequently published "The individualistic concept of the plant association" (1926), which at least received a half-day session at the Ecology Section of the International Congress of Plant Sciences, in August. There, he was attacked by Professor George Nicols (1882–1939) of Yale (Nichols 1929, Burgess 1996:81). Nichols had published two versions of a classification of plant associations (1917, 1923), based upon his survey of vegetation on Cape Breton Island, Nova Scotia (1918). At the Congress he let Gleason read his talk before giving it, and so Gleason was able to respond (1929). Gleason's sin, according to his biographer (Nicolson 1990:139–140), was questioning the status quo; however, Nichols was also defending his own classification of vegetation (Nichols 1917, 1923, 1929), which was threatened by Gleason's theory.

Schröter and colleagues planned a third IPE in Switzerland for 1915, but it was delayed until 1923 due to World War I (Fischedick and Shinn 1993:112). The fourth was in Sweden and Norway in 1925, and the 19th IPE occurred in Poland in 1989. Not until after World War II did American plant ecology exert an influence in France comparable to its earlier influence in Britain (Acot and Drouin 1997).

Lucy Braun (1889–1971), from Cincinnati, received her undergraduate and graduate degrees from the University of Cincinnati and subsequently became Professor of Botany there (Stuckey 1973, Burgess 1996:18–19). She published nine articles before 1925, but because her main ecological contributions and influence came later, she will be discussed in more detail in a later part of this history.

Conclusions

Kerner's *Pflanzenleben der Danaulaender* (1863) explored what we consider ecological topics, as did other publications which followed in Germany and elsewhere. During the 1890s, in Europe and in the American Midwest, some botanists moved beyond phytogeography and physiology to explore ideas in a new science of plant ecology. Warming's *Plantesamfund* (1895) provided the strongest early explicit impetus, in London and Chicago, though Drude's work provided the stimulus in Nebraska. Insightful botany teachers Oliver, Coulter, and Bessey almost simultaneously introduced Tansley, Cowles, and Clements to this new botanical discipline. Attempts to establish named units of vegetation by Kerner, Warming, Flahault, and Schröter, and by Moss, all failed to achieve universal acceptance.

Oliver's leadership of field trips of several days duration into places in Britain and western France, and Schröter's phytogeographical tour for an international geography congress in 1908, provided examples for Tansley to organize the first International Phytogeographical Excursion in Britain, for a month in 1911, followed by Cowles and Clements' second IPE in the United States in 1913 over a longer period. These excursions provided impetus for the founding of the first two ecological societies in Britain (1913) and North America (1915). North American ecology flourished as well as European ecology did, because American and Canadian midwestern universities were still growing and could make room for a new specialty more easily than could long-established European universities. Tansley not only wrote the early history of BES (1947), he also published appreciative obituaries of Warming (1927), Cowles (1940), and Clements (1946).

There was no vegetation theory or perspective that united all plant ecologists by the mid-1920s. Nirvana was postponed.

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