

Western Science Discovers Indian Monsoonal Wetlands: Winfield S. Dudgeon and Walter T. Saxton

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ABSTRACT

The first ecological studies of Indian monsoonal wetlands were conducted by an American missionary and botanist, Winfield Dudgeon, and a British botanist, Walter Saxton. During the 1920s, both studied seasonal changes in the vegetation of depressions on the Gangetic Plain in northern India. Up to 95% of the annual precipitation in this area falls during the summer monsoon (June to September). Consequently, these depressions are flooded during and after the monsoon, and wetland vegetation is found in them. After these depressions go dry, one or more dry land vegetation types, often grassland, are found in them that persist until the next monsoon. Ecologists had not previously described such extreme intra-annual changes in vegetation. Dudgeon and Saxton developed new theoretical frameworks to describe and classify this novel kind of vegetation change. Dudgeon proposed the concept of “seasonal succession.” Saxton rejected Dudgeon’s idea that seasonal vegetation changes were a form of succession. As an alternative, Saxton proposed the concept of “mixed formations in time.” In other words, different vegetation types or phases (wetland or dry land) were found during wet and dry periods each year. Dudgeon and Saxton pioneered the study of the impacts of large water-level changes on wetlands. They demonstrated it was propagules of wetland and upland plant species in the soil that enabled them to survive seasonally adverse environmental conditions, allowing them to persist in depressions from year to year.

INTRODUCTION

“A given area [in northern India] is subject to far greater extremes of humidity than is often experienced in temperate zone habitats. 90 per cent of the rain falls in three months, from the middle of June to the middle of Septem-

ber. During the rainy period, a given area may be a wet meadow, or, if the soil becomes waterlogged and drainage is inadequate, it may, towards the close of the period, become a swamp or a lake. After the rains cease, it gradually dries, and for six months or more is capable of supporting only a xerophytic flora” (Kenoyer 1924).

Although botanists had done significant work on the taxonomy of Indian plants in the 19th Century and early 20th Century, ecological research began only in the 1920s (Barucha 1975; Singh 2011). India’s first ecologists were American missionaries trained as botanists (Winfield Dudgeon and Leslie Kenoyer) who took positions at a Christian college in Allahabad and a British botanist (Walter Saxton) who came to Ahmedabad via South Africa. Although they were familiar with various types of vegetation change, as described by Cowles (1911) and Clements (1916), these pioneering ecologists who grew up and were educated in the temperate zone were ill-prepared to make sense of the dramatic seasonal changes in vegetation found in subtropical Indian wetlands. As noted by Kenoyer (1924), there was no known temperate zone equivalent to the intra-annual changes in vegetation that occurred in the monsoonal wetlands of the Upper Gangetic Plain. Winfield Dudgeon (1920) and Walter Saxton (1922, 1924) believed that the intra-annual vegetation dynamics of monsoonal wetlands could not be accommodated in contemporary theories of vegetation change. Consequently, they had to propose new ones. Dudgeon (1920) proposed the concept of seasonal succession, while Saxton (1922, 1924) proposed mixed formations in time.

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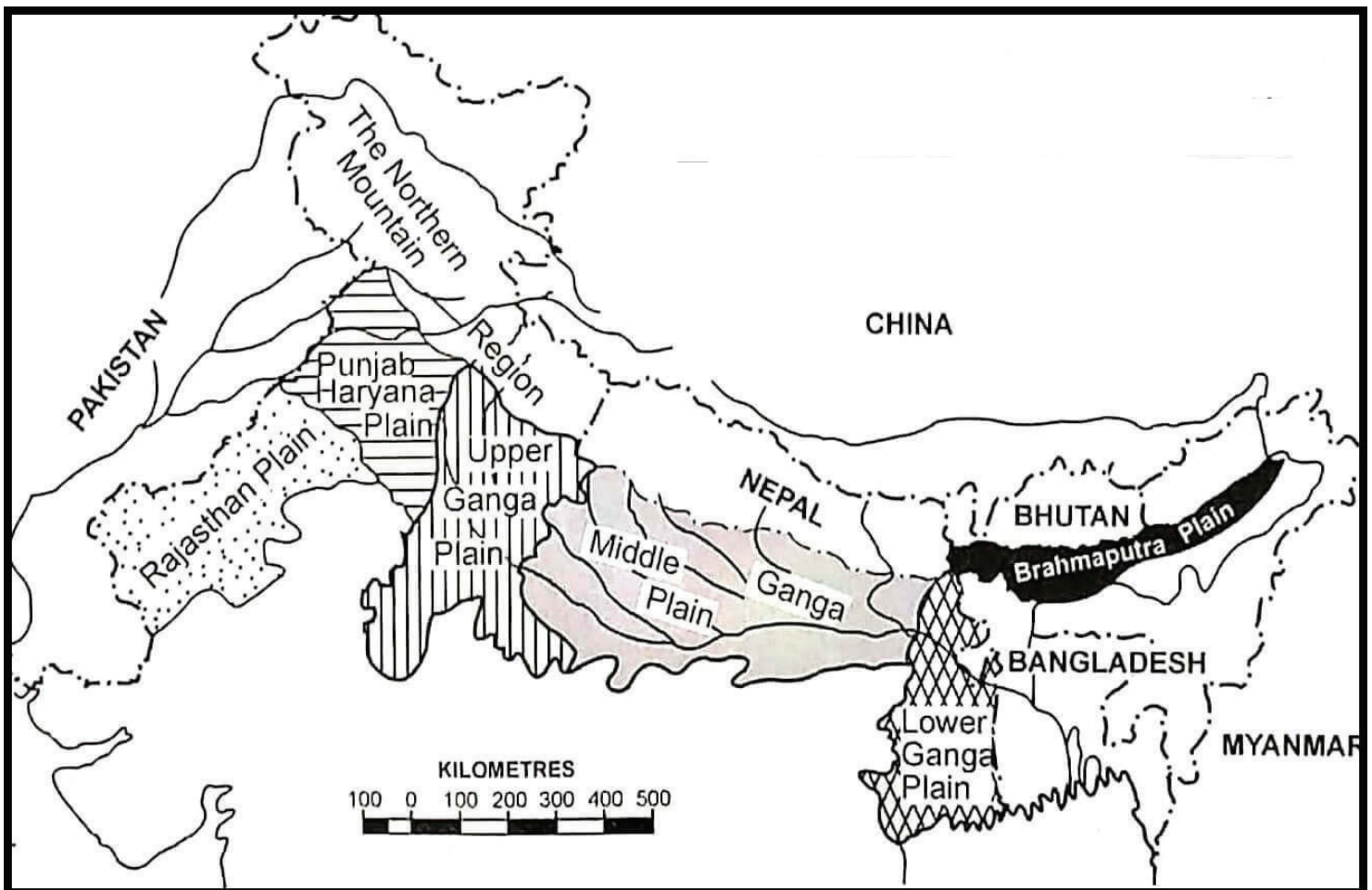


Figure 1. The Indo-Gangetic Plain and its subdivisions. Courtesy of the Union Public Service Commission of India.

MONSOONS AND MONSOONAL

The Indo-Gangetic Plain covers northern and northeastern India and parts of Pakistan and Bangladesh (Figure 1). The plain is bounded on the north by the [Himalayas](#), the source of its rivers, on the south by the [Peninsular Plateau](#), and on the east by the Bay of Bengal. This region is covered by alluvial soils deposited by its major rivers and their tributaries. The Upper Gangetic Plain, which the Ganges River and its tributaries drain, runs about 550 km east-west and 380 km north-south with an elevation between 100 to 300 m. The climate of the Gangetic Plain is subtropical, with three distinct seasons: cool (winter), hot, and rainy (monsoon) (Figure 2). Winters are cool, with average temperatures in January between 11 °C (52 °F) in the north and 15 °C (59 °F) in the southeast. It is hot and dry from mid-March to June before the monsoon's onset, and temperatures can reach 45 °C (113 °F). During the summer monsoon, which starts in June, temperatures decrease and humidity increases. Annual rainfall ranges from approximately 600 millimeters (23 inches) in the northwest to 1,300 mm (51 in.) in the southeast. The monsoon ends in mid to late September or early October. Nearly all of the region's annual precipitation (up to 95%) occurs during the summer monsoon. For more information about India's summer monsoon, see Yadav (2008).

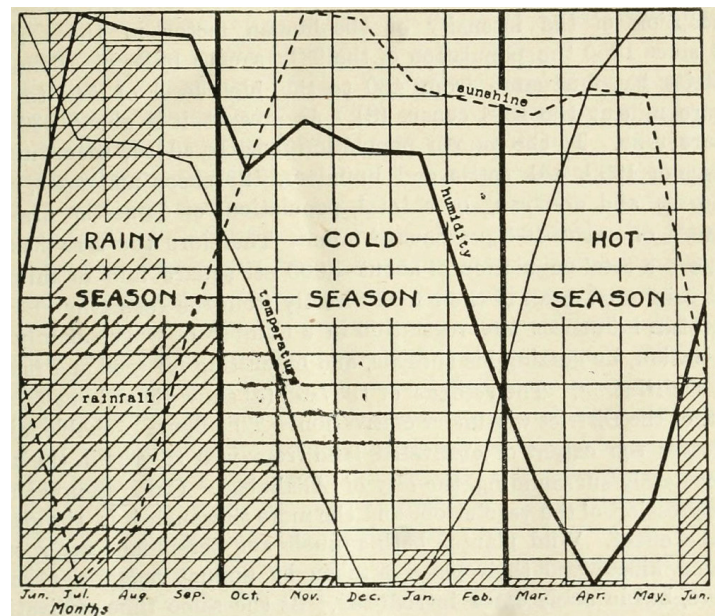


Figure 2. "Mean temperature [thin solid line], mean sunshine (mean cloudiness curve inverted) [dashed line], mean rainfall [hatched areas], and mean relative humidity [thick solid line] for the year at Allahabad, so calculated that all the maxima touch the top of the graph and the minima touch the bottom. This emphasizes the three climatic seasons [rainy, cold, and hot], which determine three corresponding vegetational seasons." (Dudgeon 1920).

The Upper Gangetic Plain has numerous shallow depressions, both natural and man-made. Because of its monsoonal climate, shallow depressions fill with water (up to 3 m deep) during the rainy season, and wetland vegetation develops. These flooded depressions gradually dry out in the following winter and spring months, and their wetland vegetation dies and decomposes, leaving only seeds and perennating organs behind. When they dry out, upland plant communities develop in these depressions. The reflooding of the depressions eliminates this upland vegetation during the next monsoon (Misra 1946; Gopal 1986). Depending on the depth of the depression, the amount of rainfall during the monsoon, grazing, and irrigation withdrawals, the length of time the depressions are dominated by wetland and upland vegetation varies from year to year, as does, to some extent, the composition of the wetland and upland vegetation (Misra 1946).

WINFIELD SCOTT DUDGEON (1886–1932)

Winfield Dudgeon (Figure 3) was born in Hedrick, IA, and died in 1932 in Ames, IA, while on leave from Ewing Christian College. He graduated from Iowa State College (now University) in 1907 and took a teaching position at Central College, Pella, IA. He did his postgraduate studies at the University of Chicago. In 1912, Dudgeon, as a missionary, went to teach at Ewing Christian College in Allahabad (Stewart 1982) and was associated with the College until his untimely death. Allahabad is in the northcentral Indian state of Uttar Pradesh at the confluence of the Ganges and Yamuna Rivers. Dudgeon founded Ewing's Department of Botany and, in 1920, was involved in the organization of the Indian Botanical Society, serving as its first president.

In 1920, Dudgeon published a paper with the uninformative title, "A contribution to the ecology of the Upper Gangetic Plain," in the *Journal of Indian Botany*. It describes the climate, geology, and vegetation within a ten-mile radius of Allahabad. He emphasized the importance and novelty of his study by noting that "For the most part, studies in plant succession have been made in temperate regions, where there is but one vegetational season, the summer or growing season. This is followed by a winter season during which the vegetation is at more or less of a standstill. In the Upper Gangetic Plain, there is no season in which growth is impossible. Growth is checked and the vegetation modified by the aridity of the hot season, and at all seasons and every stage it is interfered with even to the extinction point by the human factors." For the first time, Dudgeon documented the dramatic seasonal changes in the structure and composition of the vegetation in low-lying areas on the Gangetic Plain.

Dudgeon (1920) described his study area as "... monotonously level. Here and there are slight natural depressions that become shallow lakes during the rainy season, but which are dried up later by evaporation and by use of



Figure 3. Winfield S. Dudgeon around the time of his graduation from Iowa State College. (The Bomb, 1907, ISC Yearbook. Courtesy of the Iowa State University Digital Archives).

the water for irrigation purposes." He noted the importance of three factors controlling the distribution and composition of the vegetation in monsoonal wetlands: topography (depth of depressions), seasonal climatic changes, and human disturbances, especially grazing by domestic animals. "The climatic factors, rainfall, insolation, temperature, humidity, and air movements, are periodic in distribution, and produce three distinct seasons (Figure 2). (a) Rainy season, from the middle of June to the end of September, with high rainfall, low insolation, high temperature, and high humidity. (b) Cold season, from the first of October to the end of February, with low rainfall, high insolation, low temperature, and high humidity. (c) Hot season, from the first of March to the middle of June, with low rainfall, high insolation, high temperature, low humidity, and large air movement" (Dudgeon 1920). At Allahabad, about 94% of the annual rainfall occurs during the monsoon (rainy season).

In a depression over a year, the vegetation changes from aquatic vegetation to wet meadow to dry meadow. Dudgeon describes this as "seasonal succession." "A third type of succession is a prominent feature in a strongly periodic climate. It is illustrated by the striking changes in the

aspect and content of the vegetation from season to season and may be called seasonal succession. As a result of the three well defined climatic seasons, rainy, cold, and hot, there are three equally well marked vegetational seasons.”

Dudgeon did his postgraduate work at the University of Chicago, the home of Henry Cowles, one of the most influential early American researchers of vegetation change. To try to make sense of the intra-annual changes in monsoonal wetlands, Dudgeon turned to Cowles’ 1911 paper on vegetation cycles. Cowles (1911) is the only paper on vegetation dynamics cited by Dudgeon (1920).

There had been various models of vegetation change or succession proposed by 1920. Still, all of them had one thing in common, succession was considered an interannual, not an intra-annual, phenomenon. Clements (1916) proposed that succession is a directional and deterministic phenomenon that results in a final stage, the climax, in equilibrium with the regional climate. For Clements, succession typically took hundreds or thousands of years. Cowles (1911) described vegetation changes as nested temporal cycles (climatic, topographic, and biotic) at three different time scales: “Each climatic cycle has its vegetative cycle; each erosive [topographic] cycle within the climatic cycle, in turn, has its vegetative cycle; and biotic factors institute other cycles, quite independently of climatic or topographic change.” For Cowles, vegetation change can occur over thousands or tens of thousands of years (climatic cycles), hundreds or thousands of years (topographic/erosional cycles), and decades or centuries (biotic cycles). To Cowles’ three vegetation cycles, Dudgeon added a fourth, much shorter cycle, seasonal succession, driven by intra-annual changes in water levels.

By considering intra-annual changes in vegetation in monsoonal wetlands to be a type of succession, Dudgeon made two missteps. A successional sequence implies that every vegetation stage somehow prepared the way for the next stage. This was widely assumed to be the case in the early 20th Century (Clements 1916). However, this is not the case in monsoonal wetlands. Dudgeon also failed to differentiate his seasonal succession cycle from less extreme seasonal changes in vegetation, a feature of all kinds of vegetation. Although seasonal succession could be a logical extension of Cowles’s cyclical conception of vegetation change, Indian and other ecologists have never embraced Dudgeon’s seasonal succession (Misra 1946, see below). Nevertheless, Dudgeon described a wetland type previously unknown to European and American ecologists. He also documented the importance of water-level fluctuations for understanding wetland vegetation dynamics in India.

WALTER THEODORE SAXTON (1882–1973)

Walter Saxton was born in Great Britain and studied botany at the University of Cambridge, from which he received a Bachelor of Arts. In 1906, he became an assistant to Profes-

sor H.H.W. Pearson in the Department of Botany at South African College, Cape Town. During his seven years at South African College, Saxton published 14 papers, primarily in plant embryology and conifer taxonomy. However, during the summer of 1911–1912, he was involved in a descriptive study of the vegetation of the Manubie District, Cape Province (Saxton and Péringuey 1917). In 1913, Saxton left South Africa to accept an appointment as the professor of botany at Gujarat College in Ahmadabad, Gujarat, India. Later he held positions at Reading University and the University of Cape Town, the successor of South African College.

In 1922, Saxton published two papers on the vegetation of the Gangetic Plain. Dastur and Saxton (1922) is an unremarkable study of factors controlling the distribution of savanna species in an area near Ahmadabad. However, Saxton (1922) is a remarkable paper on seasonal vegetation changes due to north India’s monsoonal climate. Saxton’s 1922 paper was published in the *Journal of Indian Botany*, the same journal in which Dudgeon had published his 1920 paper.

Saxton (1922), in his Introduction, makes clear why he is publishing this paper: “The writer has always deprecated the action of those persons who evolve new theories, from *a priori* considerations, out of their own inner consciousness, without any material evidence to support them, as well as of those who glean some facts from half a dozen published sources, diligently select those favourable to a particular pet theory, ignore all the other facts which do not fit it and rush into print. It seems, therefore, advisable to state that the theory to be developed here has not arisen in either of these two ways. It is based mainly on some ecological work which is being carried on at the present time by the writer and some of his students. This work is likely to be continued for some months at least and meanwhile, the idea gradually crystallizing from it seemed sufficiently important, in its relation to Indian ecological problems, to justify this attempt to complete the crystallizing process. It is proposed rather to explain the idea than to give details of the facts which first led to its adoption.” Saxton’s 1924 paper “Phases of vegetation under monsoon conditions” would contain the promised data.

Saxton had an ax to grind but named no names, and his paper contains no references. He takes to task his unnamed adversary because of a failure to recognize that India’s vegetation can never be adequately described or classified using existing Western models of vegetation change. “I know of no work in recent years which has suggested any broad basis upon which detailed ecological studies in India may rest. ... The result has been that those who have tried to define Indian plant communities have quite definitely made an attempt to fit them into the systems which have evolved in the last twenty years from the ecological work done in Western countries. Those systems are already comparative-

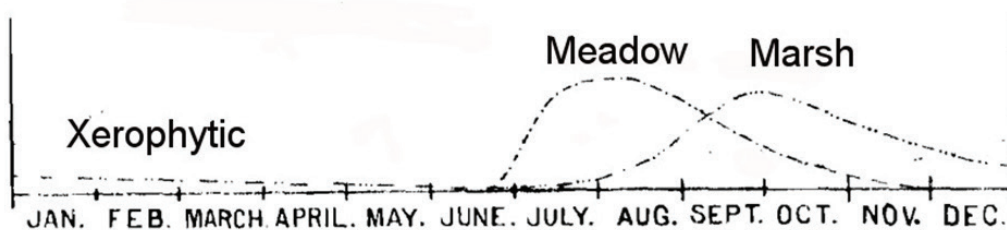


Figure 4. Annual vegetation phases (mixed formations in time) in a low-lying area on the Gangetic Plain, India. (Adapted from Saxton 1922).

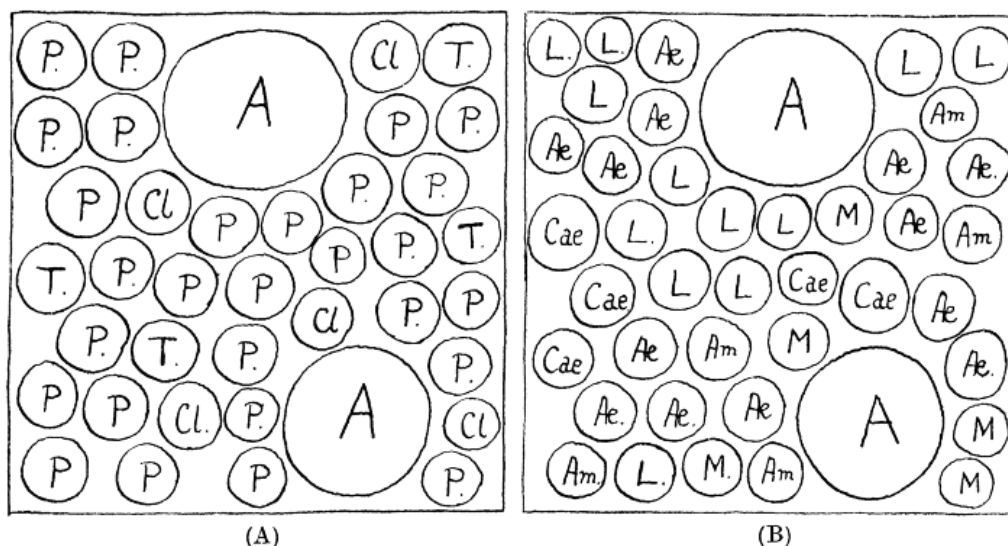


Figure 5. Idealized maps of each plant species in a small plot: (A) during the grassland phase and (B) during the marsh phase. The only species found in both vegetation phases was A — *Andropogon annulatus*. A = *Andropogon annulatus* [perennial]; Ae = *Aechynomene indica* [annual or perennial]; Am = *Ammania auriculata* [annual]. Cae = *Caesulia axillaris* [annual]; Cl = *Cleome viscosa* [annual]; L = *Ludwigia parviflora* [annual]; M = *Melochia corchorifolia* [herbaceous perennial]; P = *Panicum prostratum* [annual]; T = *Trianthema monogyna* [annual] (Saxton 1924).

ly rigid and the task of fitting our plant communities into them is not an easy one. Indeed I have come to the conclusion that it cannot be done, at least not on the lines which have been hitherto attempted” (Saxton 1922). Although not named, Winfield Dudgeon’s “seasonal succession” obviously is Saxton’s target.

Saxton (1922) goes on to make it clear why Western vegetation models are not suitable for India: “... the great difference between Europe and America on the one hand and India on the other is that the former really have no habitat which even approximately corresponds to the Indian monsoon habitat Seasonal differences are found in other habitats, but I believe it must be admitted that they are much less profound and far-reaching than those in the monsoon habitat as we see it in its typical development.” Saxton (Figure 4), like Dudgeon, recognizes significant seasonal changes in environmental conditions over a year: “... we often find that during the year two (or it may be three)

profoundly different sorts of conditions are met within the same spot. Practically, these constitute two (or three) entirely different habitats. First, a condition when both soil and air may be almost continuously water-saturated for about three months ... [Second] at the close of the monsoon, the soil and air both gradually dry, and after about a month, a period of seven months of intense and absolute drought sets in.” The vegetation found during the rainy season (some kind of wetland) has nothing in common with that of the dry season (called xerophytic by Saxton) (Figures 4 and 5).

Out of hand, Saxton dismisses the idea that monsoonal habitats undergo some form of succession: “... this is not succession as understood in Oecology. Probably this will be universally admitted and it will not be necessary to discuss the point further.” After dismissing Dudgeon’s seasonal succession without referencing it, Saxton presents his new concept: mixed formations in time. “The theory is advanced that in such an area it often happens that we cannot regard

a small and reasonably homogeneous part of it as occupied by a single unit (“formation”) of vegetation, but rather that two (or even three) entirely different plant communities regularly alternate with one another, though each persists to some extent through the dominant phases of the other, thus giving rise to the idea of “Mixed formations in time”. In other words, Saxton proposes that monsoonal depressions have two or more phases (Figures 4 and 5). However, these seasonal phase shifts are not a form of succession because one phase does not give rise to or permanently replace another. For Saxton, the various phases are independent entities that exist simultaneously. While one phase is extant, the other(s) is(are) latent. The latter exist mainly as dormant seeds and vegetative propagules until environmental conditions change sufficiently. “Mixed formation in time” was not the aptest name for Saxton’s new concept, and his 1924 paper uses the more descriptive and intuitive “vegetation phases” in its title.

The seasonal shifts in vegetation in monsoonal depressions on the Gangetic Plain described by Dudgeon (1920) and Saxton (1924) are very similar. Dudgeon (1920) better describes the region’s monsoonal climate (Figure 2), whereas Saxton (1924) better describes and illustrates the vegetation phases (Figures 4 and 5). He also notes the importance of the seed bank and vegetative propagules for enabling species to persist from year to year in a wetland. The seed banks of monsoonal wetlands would not be studied for another 60 years (Middleton et al. 1991). In an attempt to determine what anatomical and morphological adaptations allow plant species to grow in a monsoonal area, a large part of Saxton (1924) is devoted to anatomical studies of selected plant species, a common type of ecological study that started in 19th Century Germany and persisted into the early 20th Century (van der Valk 2011, 2014).

DISCUSSION

The intra-annual vegetation phases of northern Indian monsoonal wetlands are an extreme example of comparable intra-annual cycles in wetlands in other parts of the world. Others include those found in seasonal prairie wetlands in North America (van der Valk and Mushet 2016), playa wetlands in North America (Bolen et al. 1989), and monsoonal wetlands in northern Australia (Finlayson 2005). Dudgeon was born in Mahaska County, Iowa, south of the Prairie Pothole region. Still, he studied botany at Iowa State College (now University) in Ames, Iowa, which is in the Prairie Pothole region. Much of the early work on the vegetation dynamics of prairie potholes was done in Iowa, much of it close to Ames (van der Valk 1981, 2005). Ironically, Dudgeon, while a student in Ames, could have observed similar, but less extreme, seasonal changes in pothole vegetation to those he later studied in north India.

Dudgeon (1920) and Saxton (1922, 1924) described what was, for them, a new kind of wetlands that was

unknown to Western ecologists at the time. Although they studied the same wetlands, they differed in how they interpreted their intra-annual vegetation changes. Dudgeon described them as a new type of succession: “seasonal succession.” In contrast, Saxton described them as a new type of vegetation dynamic: “mixed formations in time” or “phases of vegetation.” From my perspective as someone who worked on the vegetation dynamics of monsoonal wetlands in northern India (Middleton et al. 1991, van der Valk and Middleton 2024), Saxton’s conceptualization of their vegetation dynamics as a series of vegetation phases better describes them than Dudgeon’s “seasonal succession.” However, it took 40 years for me to reach this conclusion (van der Valk and Middleton 2024). I made the mistake Saxton (1922) warned about when I began working in India in the 1980s. I interpreted the vegetation dynamics of monsoonal wetlands as a compressed habitat cycle, a type of cyclical succession found in semi-permanent prairie potholes in North America (Middleton 1999, van der Valk 1981, 2005). I studied habitat cycles in Iowa in the late 1970s and early 1980s. Habitat cycles are cyclical changes that occur over one to two decades (van der Valk 1981, 1982, 2005). In other words, I unconsciously adopted Dudgeon’s seasonal successional model in the guise of a compressed habitat cycle completed in only one year.

How much impact did Dudgeon and Saxton’s work have on the development of wetland science in India and elsewhere? Dudgeon (1920), according to Google Scholar, at the time of writing, has only been cited 36 times, mainly since the 1980s. However, Misra (1962), in a review paper on Indian vegetation studies, credits Dudgeon as the first ecologist to apply the concept of succession to Indian vegetation. However, Misra also faults Dudgeon for not taking a multiyear approach to the vegetation dynamics of monsoonal wetlands. Based on Misra’s studies of monsoonal wetlands (Misra 1946), the species composition of the vegetation of each climatically distinct part of a year (rainy, cool, hot) is very similar from year to year, e.g., the meadow vegetation in one year is very similar in composition to that in subsequent years. For Misra, no succession is occurring. Strangely, in his review paper, Misra does not cite Saxton’s papers. According to Google Scholar, Saxton (1922) has been cited only seven times, and Saxton (1924) 27 times. Saxton (1922) deserves to be recognized as a classic paper in wetland science. Its message — don’t let your past experiences close your eyes to a new reality — is as relevant today as it was in the 1920s.

After Dudgeon and Saxton, no scientific studies of monsoonal wetlands were conducted in India until the 1940s, when Ramdeo Misra (1908-1998) returned to India (Gopal 1986) after doing postgraduate research in England (Ph.D., 1937, Leeds) with the renowned wetland ecologist W. H. Pearsall. On his return to India, Misra conducted ecological studies of northern India’s low-lying lands, ponds,

and herbaceous plant populations from 1937 to 1946 (Singh 2011). These studies (Misra 1946) confirmed much of what Dudgeon and Saxton had previously described but showed that the intra-annual vegetation changes found were more complicated than previously realized. Misra laid the foundations for field and experimental ecological studies at Indian academic and other organizations (Singh 2011). After Misra, no significant new studies of monsoonal wetlands were conducted in India until the 1980s.

Dudgeon and Saxton are important, if sadly little-known and celebrated, figures in the history of wetland science. They contributed to wetland science in three significant ways. One, they made wetland science a genuinely international discipline by highlighting that there were wetland types not found in the West. Two, they pioneered the study of the impacts of water-level changes on wetlands, an important topic in contemporary wetland ecology. Three, they demonstrated that monsoonal vegetation is well adapted to large changes in water levels because propagule banks allow both wetland and upland plant species to survive either drawdowns or periods of flooding.

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