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THE SYSTEMATICS AND ECOLOGY OF SOIL ALGAE¹

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SUMMARY

Algae occur in nearly all terrestrial environments on earth and are invariably encountered both on and beneath soil surfaces. The algal flora of the soil includes members of the Cyanochloronta, Chlorophycophyta, Euglenophycophyta, Chrysophycophyta, and Rhodophycophyta. Thirty-eight genera of prokaryotic and 147 genera of eukaryotic algae include terrestrial species, the majority of which are edaphic. Whereas systematic nomenclature of blue-green algae adheres to traditional classification based upon morphological features, proper taxonomic treatment of eukaryotic soil algae is predicated on standard methods of culture and interpretation of physiological attributes, plant mass characteristics, and morphological properties of axenic clones.

While knowledge of the physiological ecology of soil algae is primarily based on laboratory evidence, it is well established that solar radiation, water, and temperature are the most important abiotic factors governing their distribution, metabolism, and life history strategies. Biotic interactions are often as important, whereas ionic factors (including pH), oxidation-reduction potential, and soil texture are less important, if only because their influences are less well understood.

Algae play an important role in primary and secondary plant community succession by acting as an integral part of the colonial synusium. The principal functional attributes of algal communities in soil include primary production, dinitrogen fixation, and stabilization of aggregates. Although as many as 10^8 algae per gram have been documented, soils commonly support between 10^3 and 10^4 per gram.

As an avenue for the incorporation of carbon and nitrogen and for minimizing erosion through stabilization of aggregates, algae are valuable in agriculture. Although manipulation of edaphic algal populations in temperate countries is of novel occurrence, their successful use in India as a means for reclaiming saline soils and as a source of fertilizer nitrogen is well documented.

Soil algae are affected by synthetic pesticides and pollutants. In general, most herbicides, fungicides, and soil fumigants are detrimental to soil algae while most insecticides are not. Algae have been utilized as biological assay organisms for anticipating crop response to both fertilizers and pesticides because of their biochemical similarity to higher plants and their quick generation time.

As future research with soil algae leads to a greater awareness of their importance in soil, it might be anticipated that manipulation of populations in agricultural systems of temperate regions will become more widespread with consideration of the potential benefits of soil algae made by scientists in other disciplines.

ZUSAMMENFASSUNG

Unter fast allen terrestrischen Bedingungen können Algen vorkommen, ganz besonders auf oder direkt unter den Bodenoberflächen. Die Algenflora auf den Böden umfaßt unter anderem Vertreter der Cyanochloronta, Chlorophycophyta, Euglenophycophyta, Chrysophycophyta und Rhodophycophyta. Acht und dreissig Gattungen prokaryotischer und 147 eukaryotischer Algen zeichnen sich durch terrestrische Arten aus, die meist edaphisch vorkommen.

Während die taxonomische Nomenklatur der Cyanochloronta noch an der auf morphologischen Kriterien beruhenden traditionellen Klassifikation festhält, basiert die beste taxonomische Behandlung der eukaryotischen Bodenalgae auf Standardmethoden der Kultur sowie der Auswertung physiologischer Kennzeichen. Morphologische Eigenschaften sollten nur von axenisch kultivierten Klonen herangezogen werden.

Obwohl unsere Kenntnis der physiologischen Ökologie der Bodenalgae weitgehend durch Laborbefunde erreicht wurde, ist doch gut belegt, daß die wichtigsten abiotischen Faktoren, die Verbreitung, Stoffwechsel und Lebensstrategie regulieren, Sonnenstrahlung, Wasser und Temperatur sind. Biotische Interaktionen sind oft von gleicher Bedeutung; Ionen-Bedingungen (einschließlich pH), Redox-Potentiale und Bodentextur erscheinen vielleicht nur deshalb weniger bedeutungsvoll, weil ihr Einfluß weniger gut verstanden wird.

Algen spielen eine entscheidende Rolle bei den primären und sekundären Pflanzensukzessionen, da sie ein integraler Teil der beginnenden Besiedlung darstellen (Kleinlebensgemeinschaften). Die wichtigsten funktionellen Beiträge der Algengesellschaften umfassen u.a. Primärproduktion, N_2 -Fixierung und Stabilisierung des Bodens. Bis zu 10^8 Algen pro Gramm wurden nachgewiesen, doch enthalten Böden pro Gramm meist zwischen 10^3 – 10^4 Individuen.

Für die Agrikultur sind die Algen wegen des Einbaus von Kohlenstoff und Stickstoff wertvoll, ebenso wegen ihrer erosionsmindernden Eigenschaften. Obwohl die Manipulation von Populationen edaphischer Algen in temperierten Gebieten noch ganz neuartig ist, wird sie erfolgreich in Indien bei der Wiederbesiedlung saliner Böden und als Quelle gebundenen (Dünger-) Stickstoffs angewendet.

Bodenalgae werden von synthetischen Pestiziden und Verschmutzungen beeinflusst. Im allgemeinen gilt, daß die meisten Herbizide, Fungizide und Bodenräuchermittel starke Wirkungen haben, viele Insektizide jedoch heine. Algen werden auch als Testorganismen zur Abschätzung der Effekte von Düngemitteln und Pestiziden auf die Kulturpflanzen verwendet, da sie biochemisch sehr ähnlich wie die Höheren Pflanzen reagieren und zudem eine kurze Generationszeit haben.

Weitere Forschung an Bodenalgien wird zur verbesserten Kenntnis ihrer Bedeutung führen und es kann erwartet werden, daß ihre Nutzung sich auch in der Landwirtschaft temperierter Zonen ausbreitet, insbesondere wenn man auch ihre mögliche Verwendung berücksichtigt, die durch Forschungen anderer Disziplinen angeregt wird.

INTRODUCTION

CATEGORIES OF TERRESTRIAL ALGAE

In 1935, J. B. Petersen, defined three categories of terrestrial algae on the basis of habitat. These were the aero-terrestrial algae, occurring on substrates elevated above the ground, the hydroterrestrial algae, growing on permanently wet soil, and the eu-terrestrial algae, including both epiterranean and subterranean forms. Tiffany (1951), defined nine categories, and by his system, edaphophytes (soil algae) included surface and subsurface forms (saphophytes and cryptophytes, respectively), while aerophytes (aerial algae) were those found on leaves (epiphylliphytes), bark (epiphloeophytes), bare rock (lithophytes), or animals (epizoo-phytes). Endophytes were defined as algae living within the tissues of other plants and endozoophytes as algae living inside of animal hosts. The algae of ice and snow were designated cryophytes. This review will primarily be concerned with those terrestrial algae designated by Petersen as eu-terrestrial, the edaphophytes of Tiffany. The ecology of hydroterrestrial algae and of lithophytes will also be considered.

The earliest review of literature on soil algae appeared as a monograph by the Danish botanist J. B. Petersen (1935), which included a comprehensive integration of previous knowledge together with his own observations and experimental results. A 1964 review by Shields and Durrell entitled *Algae and Soil Fertility* is the most recent collection of knowledge on soil algae in the English language. In 1969, a book written by M. M. Gollerbakh (or Hollerbakh) and E. A. Shtina entitled *Soil Algae* was published in Russian. It included eleven chapters on history, habitat, methods, population and community ecology, agricultural aspects, and dinitrogen fixation. English translations of references to the Soviet literature have been compiled (Forest, 1965; Cameron, 1974).

HISTORICAL DEVELOPMENT AND FLORISTIC LISTS

Petersen (1935) noted that Lyngbye (1819) had credited Paracelsus, an ancient Greek, as having recorded the earliest known reference to a soil alga, probably a species of *Nostoc* Vaucher. Dillenius (1741) included in his monograph a description of *Nostoc commune* Vaucher from soil. Modern investigation was initiated by Vaucher (1803), Dillwyn (1809), Agardh (1812, 1817), and Lyngbye (1819), all of whom included descrip-

tions of soil algae in works dealing with plant taxonomy. During the mid-19th century, Kützing (1845–1871), Ehrenberg (1843, 1854), and Rabenhorst (1863) authored taxonomic works which included descriptions of species of algae from soil. It was during this period that descriptions by Fries (1825), of *Chlorococcum humicola*, and Ehrenberg (1843), of *Hantzchia amphioxsis* and *Pinnularia borealis* were made.

Primary interest in soil algae was of a taxonomic nature through the early 20th century. Monographs by Bornet and Flahault (1886–1888), and Gomont (1892) on the Cyanophyceae, by West and West (1897, 1904) on desmids, by Heering (1907, 1921) on *Vaucheria* deCandolle, and Geitler (1925, 1932) on the Cyanophyceae were among the many works in which descriptions of species of soil algae appeared. Kolbe (1932) credited Deby (1879) for observing that certain groups of algae inhabited soil to the near exclusion of true aquatic situations. Thereafter, as phrased by Petersen (1935), investigations of soil algae became floristic-ecological in nature.

The first compilation of a species list which included soil algae was by Graebner (1895), who described heath communities of Northern Germany. He justified inclusion of descriptions of soil algae on the basis of their value as pioneer species on poorer soils of the region. To date, species lists have been published for widely separated areas, and while taxonomic incongruities prevent direct comparisons between earlier and later compilations, they are included here both as an indication of the amount of attention given to soil algae and as a starting point for contemporary studies.

Lists of soil algae have been compiled from **England** (Fritsch, 1907a; Fritsch and Salisbury, 1915; Bristol-Roach, 1927a; James, 1935; Fritsch and John, 1942; John, 1942; Lund, 1945, 1947; Broady, 1979a), **Wales** (Allen, 1971), **France** (Frémy, 1925; Chodat and Chastain, 1957), **Denmark** (Petersen, 1932a, 1935), **Greenland** (Petersen, 1928, 1935), **Iceland** (Petersen, 1928, 1935; Broady, 1978), **Belgium** (Compère, 1966) **Switzerland** (Vischer, 1945), **Germany** (Graebner, 1895), **Germany and Scandinavia** (Esmarch, 1911, 1914; Gistl, 1933; Koffman, 1934; Fehér, 1936, 1948), **Italy** (Trenkwalder, 1975), **Hungary** (Komaromy, 1975, 1976, 1977), **Romania** (Grintzesco, 1929; Gruia, 1970a, 1970b, 1971, 1973; Ionescu-Teculescu and Chirila, 1971), **Yugoslavia** (Ercegovic, 1925; Schwarz, 1979), **Bulgaria** (Aleksiyeva, 1960; Draganov, 1964), **Portugal** (De-Menezes, 1973), and the **Soviet Union**, including **RUSSIA AND TURKMENIA** (Bolshev and Manucharova, 1947; Gollerbach, 1953; Gollerbach et al., 1956; Shtina, 1957; Bolshev and Shtina, 1959; Shtina and Bolshev, 1960, 1963; Bolshev, 1952, 1968; Aleksakhina, 1971; Desortova, 1974; Busygina, 1976; Chanlygina, 1975, 1976; Domracheva, 1977; Osmanova and Sdobnikova, 1977; Berman et al., 1978), **PAMIR** (Odintsova, 1941; But, 1967), the **UKRAINE** (Vizhikovsoka, 1953; Prykhod'kova 1971), **ES-**

TONIA (Riis, 1972), KAZAKSTAN (Troitskaya, 1965; Sdobnikova, 1967), TADZHIKISTAN (Melnikova, 1955; Markova, 1974), and SIBERIA (Gromov, 1957; Androsova, 1964).

Lists from other countries include those compiled for **North Africa** (Killian and Fehér, 1939); **Senegal** (Roger and Reynaud, 1976); **Zaire** (Duvigneaud and Symoens, 1950); **Israel** (Friedmann et al., 1967); **Pakistan** (Ali and Sandhu, 1972); **India** (Ghose, 1923; Banerji, 1935; Singh, 1939; Gonzalves and Gangla, 1949a; Mitra, 1951; Dutta and Venkataraman, 1958; Marathe, 1965; Pandey, 1965; Raju, 1972; Anantani and Marathe, 1972a; Marathe and Anantani, 1972; Tiwari, 1972; Kamat and Patel, 1973; Marathe and Khushaldas, 1975; Ali et al., 1978), **Sri Lanka** (Fritsch, 1907b), **Malaysia** (Johnson, 1962a, 1969; MacEntee et al., 1973), **Singapore** (Johnson, 1974a), **Indonesia** (Johnson, 1974b), **Japan** (Akiyama, 1961, 1965), **New Guinea** (Johnson, 1962b); the **Marshall Islands** (Whitton, 1971; Arvik and Willson, 1974); **Fiji**, **Moorea**, **American Samoa**, and **Tahiti** (MacEntee et al., 1973); **New Zealand** (Flint, 1958; MacEntee et al., 1973); **Australia** (Moewus, 1953; Bunt, 1954; MacEntee et al., 1973); and **Antarctica** (Fukushima, 1959; Flint, 1960; Drouet, 1962a; Holm-Hansen, 1964; Cameron, 1966, 1969a, 1971, 1972a; Cameron and Benoit, 1970).

Countries in the Western Hemisphere for which species lists have been compiled include **Argentina** (Tell, 1971a, 1971b, 1973, 1976; DeHalperin et al., 1976; Sagardoy, 1977); **Chile** (Forest and Weston, 1966; Cameron et al., 1966); **Venezuela** (Balloni and Materassi, 1968); **Jamaica** (Herndon, 1958a, 1958b; Durrell, 1963a); **Cuba** (Arce, 1956; Arce and Bold, 1958; Martínez-Vera, 1975); **San Miguel Island and the Yucatán (México)**, **Tobago**, **Guyana**, **Surinam**, **Colombia**, and **Ecuador**, including the Galápagos (Durrell, 1963a; Archibald and Bold, 1975); **Guatemala**. (Durrell, 1963a); **Costa Rica** (Durrell, 1963a; Archibald, 1972a); **San Andreas Isle** (Archibald, 1972a); **Canada** (Lowe and Moyse, 1934), and the **United States**, including **ALABAMA** (Blackwell, 1963; Cox, 1967; Deason, 1969), **ALASKA** (Cameron, 1970); **ARKANSAS** (Couch, 1942); **ARIZONA** (Cameron, 1958, 1960, 1961, 1963a, 1964a, 1964b; Markey and Hevly, 1974); **CALIFORNIA** (Drouet, 1943; Durrell, 1962); **COLORADO** (Robbins, 1912; Durrell, 1959); **CONNECTICUT** (Hilton and Trainor, 1963); **FLORIDA** (Smith and Ellis, 1943; Smith, 1944; Brannon, 1945; Arirk, 1970; Norton and Davis 1975); **HAWAII** (MacEntee and Bold, 1978; Carson and Brown, 1978); **NEVADA** (Drouet, 1958, 1960; Shields and Drouet, 1962; Hunt and Durrell, 1966); **NEW JERSEY** (Hunt et al., 1979), **NORTH CAROLINA** (Wylie and Schlichting, 1973); **NORTH DAKOTA** (Nordin and Blinn, 1972); **OHIO** (Coyle, 1935); **OKLAHOMA** (Willson and Forest, 1957; England, 1958; Willson, 1958; Forest, 1962); **PENNSYLVANIA AND NEW JERSEY** (MacEntee, 1970; MacEntee et al., 1973; MacEntee and Bold, 1974); **TENNESSEE** (Forest, 1962; Hofstetter, 1968; Cox and Hightower, 1972); **TEXAS** (Cain, 1964; Dykstra,

1966; Archibald, 1969; Milliger, 1969; Dykstra et al., 1975; King and Ward, 1977; MacEntee and Bold, 1978); UTAH (Martin, 1939, 1940); WASHINGTON (Metting and Rayburn, 1979a; Metting, 1979); and WISCONSIN (Olson, 1961; King, 1975a, 1975b).

Compilation of floristic lists is accomplished either by direct microscopic examination of algal growth on soil or by one of a number of indirect methods whereby the presence of algae in a sample of soil is implicated following growth in an enriched medium. The earliest lists, compiled during the 19th century, were the result of direct examination of soils prepared as pastes, and treated with popular stains. The buried slide technique, a variation introduced by Chlodny (1930), which while indicating spatial relationships (Lund, 1947; Evans, 1959), also allows quantification of numbers of cells or individuals per weight of soil when a carefully pre-weighed slide is employed (Verplanke, 1932). More recent methods of a direct nature include suspension of a known quantity of soil in molten agar in a counting chamber (Jones and Mollison, 1948), the observation of chlorophyll fluorescence (Tchan, 1952; Sharabi and Pramer, 1973; Drew and Anderson, 1977), and sectioning of soil following impregnation with resin (Jones and Griffiths, 1964). While much has been learned by means of direct observation of algae in soil, systematic study of the physiological and community ecology of soil algae has followed development of methods for culturing algae in the laboratory.

CULTURING SOIL ALGAE

Publications which include information pertaining to the cultivation of algae from soil include those by Bold (1942), Pringsheim (1946a), Brunel et al. (1950), Smith (1951), Kratz and Myers (1955), Provasoli and Pitner (1959), Smith and Wiedeman (1964), Wiedeman (1964), Stein (1973) and Starr (1978).

Enrichment cultures are prepared by placing soil samples into laboratory media under conditions of incubation which promote germination of resting stages and enhance vegetative growth. The first enrichment experiments intended to promote growth of soil algae were by Graebner (1895), who placed soil in flasks containing sterile soil and demineralized water. Jacobsen (1910) inoculated soil into nutrient media containing fibrin, albumin, gluten, and casein in order to promote growth of algae. Esmarch (1911, 1914), placed sterile filter paper over moistened soil in a culture dish and recorded observations of algal growth which penetrated the fibers. Enrichment cultures prepared by Robbins (1912), Petersen (1915), Bristol (1919a), and Moore and Karrer (1919), were among the earliest in which samples of soil were added to solutions of mineral salts. Durrell and Shields (1961), introduced a variation in which sand was slanted in order to create a gradient of moisture.

Commonly employed as an enrichment medium for soil algae is the soil-water culture (De, 1939; Pringsheim, 1946b, 1950; Cameron et al., 1965; Starr, 1978). By this method, soil samples (or dilutions) are added to tubes or flasks which contain soil overlaid with water or a mineral solution and have been autoclaved or tyndallized. The growth of different species can be elicited by manipulation of the enrichment conditions. Relatively dilute concentrations of mineral salts favor the growth of blue-green algae, whereas a more concentrated medium, or one with a greater variety of nutrients enhances the growth of diatoms and/or green and yellow-green algae (Pringsheim, 1950). Addition of organic compounds may result in greater representation by euglenoids (Pringsheim, 1950). By adjusting incubation temperatures to 35°C, the growth of blue-green algae is favored, while dinitrogen-fixing species can be isolated in media free of combined nitrogen (Allen and Stanier, 1968).

Cultures may be used to quantify populations of algae in soil by preparing successive dilutions of a known amount of soil, either in water or an enrichment solution (Bristol-Roach, 1927a, 1927b). The major variation on the dilution technique of Bristol-Roach is the plate count method in which aliquots are removed from dilution vessels and spread on the surface of a solidified medium. While Beijernick (1889) employed gelatin and Richter and Orłowa (1928) utilized a silicic acid jelly permeated with inorganic salts, recent investigators have used agar as the solidifying agent.

The establishment of unialgal and axenic cultures of algae is essential for the proper taxonomic treatment of eukaryotic microalgae (Bold, 1970). Beijernick (1890), was the first to obtain pure cultures of green algae. The first axenic cultures of diatoms were obtained by Miguel (1892), the first blue-green algae by Pringsheim (1914), and Glade (1914). Much early success was the result of careful manipulation using sterile technique (Skinner, 1932a; Wilson, 1937). Wilson and Westgate (1943) introduced the now widely used centrifugation method for separating algae from bacteria. Variations on the technique have been described by Brown and Bischoff (1962) and Wiedeman et al. (1964). Although this method has been used with success to obtain pure cultures of eukaryotic algae, the purification of blue-green algae is more difficult. Micromanipulation was used by Bowyer and Skerman (1968) to enhance the process whereby the cyanophyte "cleans" itself by gliding through softened agar. Gerloff et al. (1950), obtained pure cultures of blue-green algae by repeated sub-culturing and exposure to ultraviolet radiation, a method later used by Allison et al. (1937) and Mehta and Hawxby (1978). Purification of cyanophytes on silica acid gel (Pringsheim, 1914), in chlorine water (Fogg, 1942; DeHalperin et al., 1973), and with antibiotics (Pinter and Provasoli, 1958; DeHalperin et al., 1973; Reynaud and Roger, 1977) are among the

techniques outlined by Singh (1961). Bednarova et al. (1976), listed optimal concentrations of antibiotics for the elimination of bacteria and fungi from algal cultures. Singh and Satyanarayana (1968) followed ultraviolet irradiation with a HgCl_2 treatment. McDaniel et al. (1962) were successful in purifying blue-green algae with detergents and phenol. Krauss (1966) used gamma irradiation from a ^{60}Co source for the same purpose. Allen (1952), and Stanier et al. (1971), advised purification of blue-green algae be attempted by repeated subculturing of fragments from the periphery of fast-growing plant masses as a means of avoiding mutation from chemical or radiation methods.

THE SYSTEMATICS OF SOIL ALGAE

GENERAL CONSIDERATIONS

The algal flora of the soil includes members of the following major Divisions (sensu Bold and Wynne, 1978): Cyanochloronta (blue-green algae), Chlorophycophyta (green algae), Chrysophycophyta (diatoms and yellow-green algae), Euglenophycophyta (euglenoids), and Rhodophycophyta (red algae). Most soil algae, both in kind and number, are members of the Cyanochloronta and Chlorophycophyta, many belong to the Chrysophycophyta, and a few to the other two divisions.

Methods of study and nomenclatural problems associated with soil algae are shared with freshwater species, although it is well known that certain taxa (species, genera, and in some cases orders) are peculiar to edaphic situations (Bold, 1970). Most phycologists now adhere to the opinion that proper taxonomic treatment of soil and freshwater microalgae be based on prolonged study of unialgal and pure cultures under standard laboratory conditions (Bold, 1970), although as late as 1963 it was argued that sufficient data for taxonomic treatment could be obtained from herbarium specimens (Hoek, 1963). The availability of living cultures of soil algae allows critical evaluation of the morphological and physiological attributes upon which taxa have been erected. In order to ensure that a living record of the diversity of algae be available, a number of culture collections have been established around the world (Hindák, 1970; Carr and Whitton, 1973; Ettl, 1976; Gärtner, 1976; Starr, 1978).

PROKARYOTIC SOIL ALGAE

Members of the Cyanochloronta have been regarded both as bacteria and plants, and have been classified in the Kingdom Monera (=Procar-yota) or in the Kingdom Plantae, in either the Division Schizophyta (bacteria) or the Division (or Class) Cyanochloronta (=Cyanophyta = Cyanophyceae = Myxophyceae). They are commonly referred to as

blue-green algae, blue-green bacteria, cyanophytes, myxophytes, or cyanobacteria. Blue-green algae possess some internal membranes, but lack membrane-bound nuclei, plastids, and mitochondria, and are, in these respects, bacteria-like. Other bacterial characteristics of the blue-green algae include cell wall structure and chemistry, 70S ribosomes, and details of cell division. Eukaryotic, plant-like features include pigmentation and biochemistry of photosynthesis (Bold and Wynne, 1978). Stanier et al. (1978) proposed that bacterial nomenclature be employed for taxonomic treatment of cyanobacteria.

Classification of the blue-green algae into taxonomic categories below the level of the division and class has not been agreed upon; having in fact been described as being in a state of chaos (Whitton, 1969). Traditional classification on the basis of cellular organization and the morphology of the plant mass is being challenged by microbiologists and phycologists who point out that these criteria are, to a large extent, dependent upon environmental conditions and do not reflect phylogenetic relationships upon which modern taxonomic schemes are, ideally, based. The fact that microenvironmental and climatic factors are responsible for wide morphological variation within taxa of coccoid and filamentous blue-green algae has been demonstrated (Drouet, 1962b, 1963, 1964, 1968, 1973; Drouet and Daily, 1956; Cameron, 1963b; Cameron and Blank, 1966a; Forest and Khan, 1972). Ecotypic variation, or the existence of ecophenes within species from soil was discussed by Cameron and Blank (1966a), who estimated that only about 16 species of blue-green algae constitute the total floristic diversity in hundreds of samples from hot and cold deserts around the world. For example, they reported that synonyms for *Schizothrix calcicola* (Ag.) Gomont, may number as many as 56, scattered among nine genera.

Attempts to standardize classification of the blue-green algae, based on genotypic characters, as reflected in pure culture under defined laboratory conditions, have been made (Forest et al., 1959; Kantz and Bold, 1969; Stanier et al., 1971; Ocampo, 1973). However, before standardized methods become routine, the art of rendering blue-green algae free of other life forms, without inducing mutation, must be improved. Until such time, it has been suggested that the classical system proposed by Geitler (1932) be employed (Fogg et al., 1973; Carr and Whitton, 1973). It is on this basis that references to treatments of species of blue-green algae are organized in Table II.

EUKARYOTIC SOIL ALGAE

In the last twenty years a number of new genera of eukaryotic microalgae have been erected, and while workers on both sides of the Atlantic have based their descriptions on careful study of laboratory cultures and

interpretation of the literature, there remains some debate as to which criteria are important for distinguishing taxa. For this reason, the entries in Table II and construction of the diagrammatic keys in Figures 1 through 7 include taxa from both the American and German schools.

In 1953, Silva and Starr argued that traditional methods for the taxonomic treatment of plants did not allow for adequate characterization of eukaryotic microalgae. They proposed that the genus *Chlorococcum* Meneghini be conserved on the basis of an 1847 description of *C. infusionum* (Schrank) Meneghini, in which the form of the chloroplast was considered. This choice was made in view of the fact that the original generic description by Fries (1825), was vague. Until recently, scientists working with what likely were mixed cultures of microalgae, gave the name *Chlorococcum humicola* Fries to the great majority of spherical, unicellular algae. It is currently recognized that there are about 20 genera of soil algae, included in three or four orders, which, during one or more phases of their life histories, would fit Fries original description. As a consequence, Starr (1955), proposed that in addition to chloroplast shape and number, the genera of unicellular green algae be delimited on the basis of the presence or absence of pyrenoids, and on the presence or absence of a cell wall surrounding the zoospore, as determined by inspection of its "behavior" upon quiescence. These criteria were extended by Herndon (1958a), to packet- and tetrad-forming (sarcinoid) algae, which in addition to zoosporogenesis and autosporogenesis by eleutheroschisis (successive bipartition and progressive cleavage), exhibit somatic cell division by means of desmoschisis (vegetative cell division), as defined by Groover and Bold (1969), and summarized by Bold and Wynne (1978). The establishment of firm generic criteria for palmelloid, azoosporic, and vesicular and *Characium*-like green and yellow-green algae has yet to be made. In Table I are summarized those properties of the individual plant and of the plant mass which have become standard criteria for descriptions of species, although no one has accompanied descriptions of species new to science with documentation of all of the supplementary physiological attributes.

Most of the common, and some of the uncommon genera of eukaryotic algae which have been reported to occur in soil are listed, together with references to treatments of species, in Table II. Diagrammatic keys to genera of green and yellow-green algae are organized into Figures 1 through 7.

PHYSIOLOGICAL ECOLOGY OF SOIL ALGAE

GENERAL CONSIDERATIONS

Acceptance of algae as bona fide soil microorganisms evolved in the late 19th century when it was first recognized that certain groups of

Table I
Taxonomic criteria at the species level for microalgae from soil.

Morphology of individual organisms:
Type of cell division.
Vegetative form (unicell, coenobe, filament, etc.).
Shape and number of plastids.
Presence of, number, and morphology of pyrenoids.
Morphology and behavior of zoospores.
Number and location of nuclei.
Physiological attributes of clones:
Comparative immunology.
Extracellular enzyme production.
Facultative heterotrophy (photoheterotrophy and chemoheterotrophy).
Growth at low oxygen tensions.
Growth in complex microbiological media.
Growth in the presence of antibiotics and stains.
Growth factor requirements.
Morphology and color of the plant mass on agar:
Size and shape of the plant mass.
Color change upon nitrogen depletion.
Presence or absence of a colonial mucilage.

species were restricted to soil. The concept of algae as misplaced freshwater organisms is due to the fact that aquatic forms are more readily noticed, and that gradations between planktonic, hydroterrestrial, and terrestrial microenvironments are subtle. Interpretation of edaphic algae as soil microorganisms is more widespread today, because of the realization that, as a component of the soil microflora, algae act as a reserve for plant nutrients, as organisms influencing soil structure and the activities of other organisms, and as agents for the incorporation of organic carbon and nitrogen through photosynthesis and dinitrogen fixation.

The genotype of each alga dictates the rates of their activities in relation to climatic and microenvironmental factors within or upon the soil. Little information exists about the extent to which resident populations of algae adjust their activities to compensate for fluctuating nutrient availability, quality and intensity of solar radiation, moisture, temperature, pH and ionic strength, oxidation-reduction potential and the composition of the soil atmosphere, pressure, the presence of associated microorganisms and plant roots, or the degree to which algal community structure is related to relatively static factors such as soil structure, texture, bulk density, compaction, pore size distribution, and clay minerology. Almost all ecological investigations of algal growth in soil have been of an indirect nature and limited to single or infrequent samplings, both of algal populations and associated physical, chemical, and biological factors. Therefore, our understanding of the ecophysiological nature of soil algae is based upon laboratory experiments and empirical observations.

Table II
Algal genera which include species of soil algae.

Major taxonomic category (after Bold and Wynne, 1978, and Smith, 1950)	
Genus	References to species
CYANOCHLORONTA	
CHROOCOCCALES	
<i>Anacystis</i> Meneghini	Daily, 1942 Padmaja and Desikachary, 1968
<i>Aphanothece</i> Nägeli	Geitler, 1932; Padmaja, 1972
<i>Aphanocapsa</i> Nägeli	Padmaja, 1972
<i>Chlorogloeopsis</i> Mitra & Pandey	Mitra and Pandey, 1966
<i>Chroococcidiopsis</i> Geitler	Friedmann, 1961
<i>Chroococcus</i> Nageli	Daily, 1942; Padmaja, 1972
<i>Gloeocapsa</i> Kützing	Geitler, 1932; Padmaja, 1972
<i>Gloeothece</i> Nägeli	Geitler, 1932
<i>Synechocystis</i> Sauvageau	Geitler, 1932; Copeland, 1936
OSCILLATORIALES	
<i>Anabaena</i> Bory	Geitler, 1932; Kantz and Bold, 1969; Tiware, 1972
<i>Anabaenopsis</i> Woloszynska	Geitler, 1932
<i>Aulosira</i> Kirchner	Daily, 1943; Raju, 1964
<i>Calothrix</i> Agardh	Geitler, 1932; Tiware, 1972
<i>Camptylonema</i> Schmiddle	Geitler, 1932 Prasad and Srivastava, 1964
<i>Cylindrospermum</i> Kützing	Geitler, 1932; Durrell, 1963b
<i>Desmonema</i> Berkley & Thwaites	Geitler, 1932
<i>Fischerella</i> (Bornet & Flah.) Gomont	Geitler, 1932
<i>Fremyella</i> J. de Toni (= <i>Microchaete</i>)	Geitler, 1932
<i>Hapalosiphon</i> Nägeli	Geitler, 1932; Tiware, 1972
<i>Hydrocoleum</i> Kützing	Drouet, 1943
<i>Hyphomorpha</i> Dutt, Datta & Gupta	Dutt et al., 1976
<i>Lyngbya</i> Agardh	Geitler, 1932; Baker and Bold, 1970
<i>Mastigocladus</i> Cohn	Geitler, 1932
<i>Microcoleus</i> Desmazieres	Geitler, 1932
<i>Nostoc</i> Vaucher	Geitler, 1932; Kantz and Bold, 1969
<i>Nodularia</i> Mertens	Geitler, 1932
<i>Oscillatoria</i> Vaucher	Geitler, 1932; Baker and Bold, 1970
<i>Phormidium</i> Kützing	Geitler, 1932
<i>Plectonema</i> Thuret	Geitler, 1932
<i>Porphyrosiphon</i> Kützing	Geitler, 1932
<i>Schizothrix</i> Kützing	Geitler, 1932

Table II
Continued.

Major taxonomic category (after Bold and Wynne, 1978, and Smith, 1950)	
Genus	References to species
<i>Scytonema</i> Agardh	Geitler, 1932
<i>Scytonematopsis</i> Kisselewa	Gupta, 1955; Pandey and Mitra, 1972
<i>Stigonema</i> Agardh	Geitler, 1932
<i>Tolypothrix</i> Kützing	Geitler, 1932
<i>Westiella</i> Borzi	Geitler, 1932
<i>Westiellopsis</i> Janet	Janet, 1941; Bai, 1972
<i>Wollea</i> Bornet & Flahault	Geitler, 1932
CHLOROPHYCOPHYTA	
VOLVOCALES	
<i>Chlamydomonas</i> Ehrenberg	Ettl, 1976
<i>Chlorogonium</i> Ehrenberg	Pringsheim, 1969
<i>Chloromonas</i> Gobi	Cox and Deason, 1969
<i>Heterochlamydomonas</i> Cox & Deason	Cox and Deason, 1969; Langford and Cox, 1971
TETRASPORALES	
<i>Asterococcus</i> Scherffel	Ettl, 1964a; Nováková, 1964; King, 1971
<i>Chlorogloea</i> Mitra	Mitra, 1959
<i>Chloronomala</i> Mitra	Mitra, 1959; Groover and Bold, 1969; King, 1971
<i>Gloeococcus</i> Braun	Lund, 1957; King, 1973
<i>Gloeocystis</i> Nägeli	Fott and Nováková, 1971; King, 1971
<i>Gloeodendron</i> Korschikoff	King, 1971
<i>Hormotila</i> Borzi	Trainor and Hilton, 1964
<i>Hormotilopsis</i> Trainor & Bold	Trainor and Bold, 1953; Arce and Bold, 1958
<i>Ourococcus</i> (Grobety) Chodat	Bischoff and Bold, 1963
<i>Palmella</i> Lyngbye	King, 1971
<i>Palmellopsis</i> Korschikoff	King, 1971
<i>Palmogloea</i> Kützing	Fott and Nováková, 1971
<i>Pseudogloeocystis</i> King	King, 1971
<i>Sphaerello cystis</i> Ettl	Ettl, 1964b; Nováková, 1964
CHLOROCOCCALES	
<i>Ankyra</i> Fott	Fott, 1957; Lee and Bold, 1974
<i>Ascochloris</i> Bold & MacEntee	Bold and MacEntee, 1974
<i>Bracteacoccus</i> Tereg	Starr, 1955; Bischoff and Bold, 1963; Friedmann and Ocampo-Paus, 1966; Schwarz, 1979

Table II
Continued.

Major taxonomic category (after Bold and Wynne, 1978, and Smith, 1950)	
Genus	References to species
<i>Centrosphaera</i> Brozi (= <i>Kentrosphaera</i>)	Bristol-Roach, 1927a Moore and Carter, 1926; Smith, 1950
<i>Characium</i> A. Braun	Kanthamma, 1940; Lee and Bold, 1974; Metting, 1980
<i>Characiochloris</i> Pascher	Pascher, 1925; Lee and Bold, 1974
<i>Chlorococcum</i> Meneghini	Archibald and Bold, 1970a; Metting, 1980
<i>Chlorotetraedron</i> MacEntee, Bold & Archibald	MacEntee et al., 1978
<i>Chlorozebra</i> Reisigl	Reisigl, 1969; Vinatzer, 1975
<i>Dictyochloris</i> Vischer ex Starr	Starr, 1955; Geitler, 1966
<i>Dictyochloropsis</i> Geitler	Geitler, 1966
<i>Dictyococcus</i> Gerneck emend. Starr	Starr, 1955; Reisigl, 1969; Metting, 1980
<i>Halochlorococcum</i> Dangeard	Dangeard, 1965; Guillard et al., 1975
<i>Nautococcus</i> Korschikov	Korschikov, 1926; Geitler, 1942; Müller, 1953; Archibald, 1972a
<i>Neochloris</i> Starr	Archibald, 1972b Vinatzer, 1975
<i>Neospongiococcum</i> Deason	Deason and Cox, 1971; Deason, 1959, 1971, 1976
<i>Planktosphaeria</i> G. M. Smith	Smith, 1920; Starr, 1954a, 1955; Bischoff and Bold, 1963
<i>Protosiphon</i> Klebs	Bold, 1933; Thomas, 1971
<i>Pseudocharacium</i> Korschikoff	Petry, 1968; Lee and Bold, 1974
<i>Pseudodictyochloris</i> Vinatzer	Vinatzer, 1975
<i>Pseudotrochiscia</i> Vinatzer	Vinatzer, 1975
<i>Pulchrasphaera</i> Deason (= <i>Myrmecia</i>)	Tschermak-Weiss and Pless, 1949; Peterson, 1956; Deason, 1967; Vinatzer, 1975
<i>Radiosphaera</i> Snow	Starr, 1955; Ocampo-Paus and Friedmann, 1966
<i>Rhopalocystis</i> Schussnig	Schussnig, 1955; Reisigl, 1964
<i>Spongiochloris</i> Starr	Starr, 1955; Deason and Bold, 1960; Trainor and McLean, 1964
<i>Tetraedron</i> Kützing	Brunnthaler, 1915; Smith, 1926; Starr, 1954b; Koviatic, 1975

Table II
Continued.

Major taxonomic category (after Bold and Wynne, 1978, and Smith, 1950)	
Genus	References to species
<i>Trebouxia</i> de Pulmaly	Archibald, 1975
<i>Trochisciopsis</i> Vinatzer	Vinatzer, 1975; Trenkwalder, 1975
CHLOROSARCINALES	
<i>Axilosphaera</i> Cox & Deason	Cox and Deason, 1968
<i>Borodinella</i> Miller	Miller, 1927
<i>Borodinellopsis</i> Dykstra	Dykstra, 1971; Schwarz, 1979
<i>Chlorosarcina</i> Gerneck	Deason, 1959; Chantanachat and Bold, 1962
<i>Chlorosarcinopsis</i> Herndon	Herndon, 1958a; Friedmann and Ocampo-Paus, 1965; Trainor and Hilton, 1966; Groover and Bold, 1969; Metting, 1980
<i>Chlorosphaeropsis</i> (Klebs) Vischer	Herndon, 1958a
<i>Fasciculochloris</i> McLean & Trainor	McLean and Trainor, 1965
<i>Friedmannia</i> Chantanachat & Bold	Chantanachat and Bold, 1962
<i>Heterotetracystis</i> Cox & Deason	Cox and Deason, 1968
<i>Ignatius</i> Bold & MacEntee	Bold and MacEntee, 1974
<i>Planophila</i> Gerneck	Groover and Hofstetter, 1969; Watanabe, 1978
<i>Pseudodictyochloris</i>	Vinatzer, 1975
<i>Pseudotrebouxia</i> Archibald	Archibald, 1975
<i>Pseudotetracystis</i> Arneson	Arneson, 1973
<i>Spongiococcum</i> (Deason) Deason	Deason and Cox, 1971; Deason, 1971, 1976
<i>Tetracystis</i> Brown & Bold	Brown and Bold, 1964; Schwarz, 1979
CHLORELLALES	
<i>Aerospaera</i> Gerneck	Reisigl, 1964
<i>Chlorella</i> Beijernick	Shihira and Krauss, 1964; Fott and Nováková, 1969; Kessler, 1976
<i>Chloroideum</i> Nadson	Reisigl, 1964
<i>Coccomyxa</i> Schmidle	Pascher, 1915; Reisigl, 1969
<i>Eremosphaera</i> Debary	Smith and Bold, 1966
<i>Homospaera</i> Reisigl	Reisigl, 1964
<i>Jaagia</i> Vischer	Reisigl, 1964
<i>Jaagichlorella</i> Reisigl	Reisigl, 1964
<i>Lobospaera</i> Reisigl	Reisigl, 1964
<i>Lobosphaeropsis</i> Reisigl	Reisigl, 1964

Table II
Continued.

Major taxonomic category (after Bold and Wynne, 1978, and Smith, 1950)	
Genus	References to species
<i>Muriella</i> Petersen	Petersen, 1932b, 1935
<i>Muriellopsis</i> Reisigl	Reisigl, 1964; Cox, 1971
<i>Oocystis</i> Nägeli	Smith and Bold, 1966; Groover and Bold, 1969; Rehakova, 1969
<i>Oocystaenium</i> Ichimura	Ichimura, 1976
<i>Palmellococcus</i> Chodat	Chodat, 1909; Collins, 1909
<i>Planktosphaerella</i> Reisigl	Reisigl, 1964
<i>Pseudochlorella</i> Lund	Lund, 1955
<i>Pseudochlorococcum</i> Archibald	Archibald, 1970; Archibald et al., 1970
<i>Scenedesmus</i> Meyen	Smith, 1916; Chodat, 1926
<i>Scotiella</i> Fritsch	Geitler, 1964; Trenkwalder, 1975
<i>Scotiellopsis</i> Vinatzer	Vinatzer, 1975
<i>Sphaerocystis</i> Chodat	Smith, 1920; Broady, 1976
<i>Trochisia</i> Kützing	Collins, 1909; Brunnthaler, 1915
ZYGNEMATALES	
<i>Cylindrocystis</i> Meneghini	Prescott et al., 1972
<i>Mesotaenium</i> Nägeli	Prescott et al., 1972
<i>Penium</i> de Brebisson	Prescott et al., 1975
<i>Zygogonium</i> Kützing (= <i>Zygnema</i>)	Fritsch, 1916; Transeau, 1951
ULOTRICHALES	
<i>Fottea</i> Hindák	Hindák, 1968
<i>Gloeotilopsis</i> Ramanathan	Ramanathan, 1964; Deason, 1969
<i>Hormidiospora</i> Vinatzer	Vinatzer, 1975
<i>Klebsormidium</i> Silva, Mattox, & Blackwell	Heering, 1914; Mattox and Bold, 1962; Ramanathan, 1964; Deason, 1969; Silva et al., 1972
<i>Pseudoschizomeris</i> Deason & Bold	Deason and Bold, 1960
<i>Raphidonema</i> Lagerheim	Heering, 1914; Ramanathan, 1964
<i>Raphidonemopsis</i> Deason	Deason, 1969
<i>Stichococcus</i> Nageli	Grintzesco and Peterfi, 1932; Mattox and Bold, 1962; Ramanathan, 1964; Reisigl, 1964
<i>Ulothrix</i> Kützing	Heering, 1914; Mattox and Bold, 1962; Ramanathan, 1964
<i>Uronema</i> Lagerheim	Lee, 1978

Table II
Continued.

Major taxonomic category (after Bold and Wynne, 1978, and Smith, 1950)	
Genus	References to species
OEDOGONIALES	
<i>Oedocladium</i> Stahl	Beaney and Hoffman, 1968
CHAETOPHORALES	
<i>Apatococcus</i> Agardh	Printz, 1927
<i>Botryokorynae</i> Reisigl	Reisigl, 1964
<i>Cladophorella</i> Fritsch	Fritsch, 1944
<i>Desomococcus</i> Agardh	Printz, 1927
(= <i>Pleurococcus</i> = <i>Protococcus</i>)	
<i>Fritschiella</i> Iynegar	Iynegar, 1932
<i>Leptosira</i> Borzi	Reisigl, 1964
<i>Pleurastrum</i> Chodat	Printz, 1939; Deason and Bold, 1960; Groover and Bold, 1969; Metting, 1980
<i>Polysphaera</i> Reisigl	Reisigl, 1964
<i>Protoderma</i> Kützing	Tupa, 1974
<i>Trentepholia</i> Martius	Printz, 1939
<i>Rhizoclonium</i> Kützing	Faridi, 1961; Randhawa and Venkataraman, 1961
ULVALES	
<i>Trichosarcina</i> Nichols & Bold	Nichols and Bold, 1965
EUGLENOPHYCOPHYTA	
<i>Euglena</i> Ehrenberg	Leedale, 1967; Bold and MacEntee, 1973
<i>Peranema</i> Dujardin	Leedale, 1967
CHRYSOPHYCOPHYTA	
EUSTIGMATOPHYCEAE	
<i>Ellipsoidion</i> Pascher	Reisigl, 1964
<i>Pseudocharaciopsis</i> Lee & Bold	Lee and Bold, 1974
<i>Pleurochloris</i> Pascher	Reisigl, 1964
XANTHOPHYCEAE	
<i>Botrydiopsis</i> Borzi	Petrova, 1931; Pascher, 1939; Vischer, 1945; Deason and Bold, 1960; Broady, 1976

Table II
Continued.

Major taxonomic category (after Bold and Wynne, 1978, and Smith, 1950)	
Genus	References to species
<i>Botrydium</i> Wallroth	Pascher, 1939; Skvortzov, 1972
<i>Bumilleria</i> Borzi	Pascher, 1939
<i>Bumilleriopsis</i> Printz	Printz, 1914; Vischer, 1936
<i>Characiopsis</i> Borzi	Pascher, 1939; Lee and Bold, 1974
<i>Chlorellidium</i> Vischer & Pascher	Schwarz, 1979
<i>Chloridella</i> Pascher	Reisigl, 1964
<i>Gleobotrys</i> Pascher	Reisigl, 1964
<i>Heterothrix</i> Pascher	Pascher, 1939; Vischer, 1936, 1945; Vinatzer, 1975; Broady, 1976
<i>Heterotrichella</i> Reisigl	Reisigl, 1964
<i>Monocilia</i> Gerneck	Pascher, 1939
<i>Monodus</i> Chodat	Reisigl, 1964, 1969
<i>Pseudobumilleriopsis</i> Deason & Bold	Deason and Bold, 1960
<i>Tribonema</i> Borzi	Pascher, 1939
<i>Vaucheria</i> DeCandolle	Pascher, 1939; Prescott, 1938; Venkataraman, 1961a; Blum, 1972; Polderman, 1973; Rieth, 1974
BACILLARIOPHYCEAE	
<i>Achnanthes</i> Bory	Boyer, 1927; Patrick and Reiner, 1966
<i>Amphora</i> Ehrenberg	Boyer, 1927; Patrick and Reiner, 1966
<i>Colonies</i> Cleve	Boyer, 1927; Patrick and Reiner, 1966
<i>Denticula</i> (Kützing) Hustedt	Boyer, 1927; Patrick and Reiner, 1966
<i>Eunotia</i> Ehrenberg	Boyer, 1927; Patrick and Reiner, 1966
<i>Frustula</i> (Agardh) Grunow	Boyer, 1927; Patrick and Reiner, 1966
<i>Hantzchia</i> Grunow	Boyer, 1927; Patrick and Reiner, 1966
<i>Melosira</i> Agardh	Boyer, 1927; Patrick and Reiner, 1966
<i>Navicula</i> Bory	Boyer, 1927; Patrick and Reiner, 1966
<i>Nitzschia</i> Hassal	Boyer, 1927; Patrick and Reiner, 1966
<i>Pinnularia</i> Ehrenberg	Boyer, 1927; Patrick and Reiner, 1966
<i>Stauronies</i> Ehrenberg	Boyer, 1927; Patrick and Reiner, 1966
<i>Surirella</i> Turpin	Boyer, 1927; Patrick and Reiner, 1966
RHODOPHYCOPHYTA	
<i>Cyanidium</i> Geitler	Geitler, 1959
<i>Porphyridium</i> Nägeli	Sommerfeld and Nichols, 1970

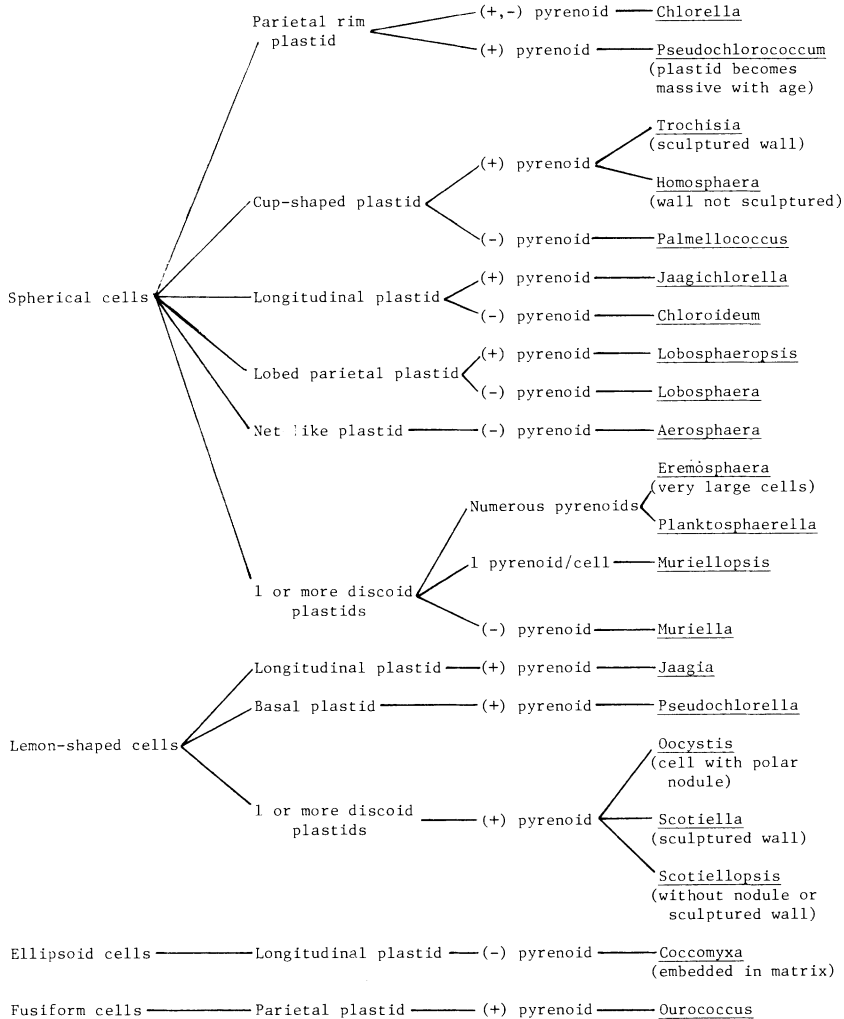


Fig. 1. Azoosporic coccoid soil algae.

NUTRITION

Most soil algae are probably photoautotrophs, that is, they utilize solar radiation as an energy source and manufacture all of their organic compounds from inorganic precursors. However, a number of soil algae belong to other nutritional categories including photoauxotrophs, which utilize solar radiation as an energy source, but are unable to synthesize all necessary organic compounds from inorganic precursors. The degree to which the algal flora is dependent upon a supply of organic growth factors

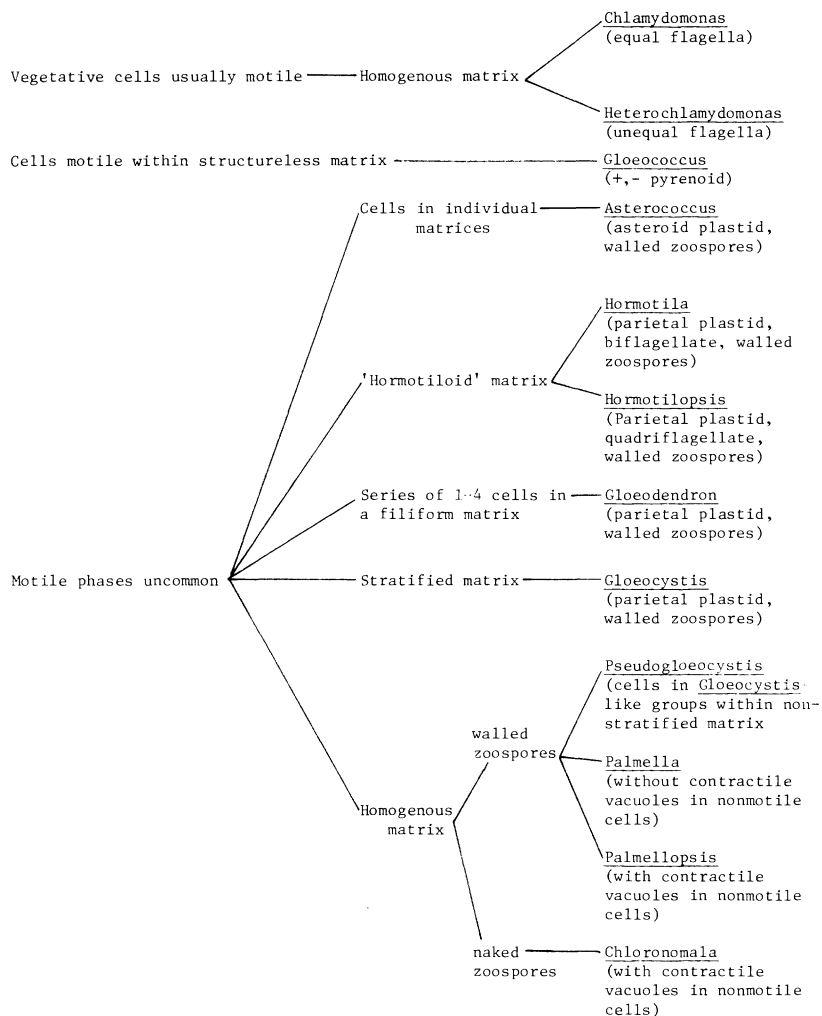


Fig. 2. Palmelloid soil algae.

from the soil cannot be accurately estimated, due to a paucity of information stemming in part from the fact that laborious and painstaking techniques must be employed in order to study growth factor requirements of microorganisms.

Colorless, chemoheterotrophic (=organotrophic) algae, such as *Pernema*, have been reported as occurring in soil (Forest, 1962; Cain 1964), although the frequency of the reports indicates that these algae are probably not important to either energy or nutrient transformations. The fact

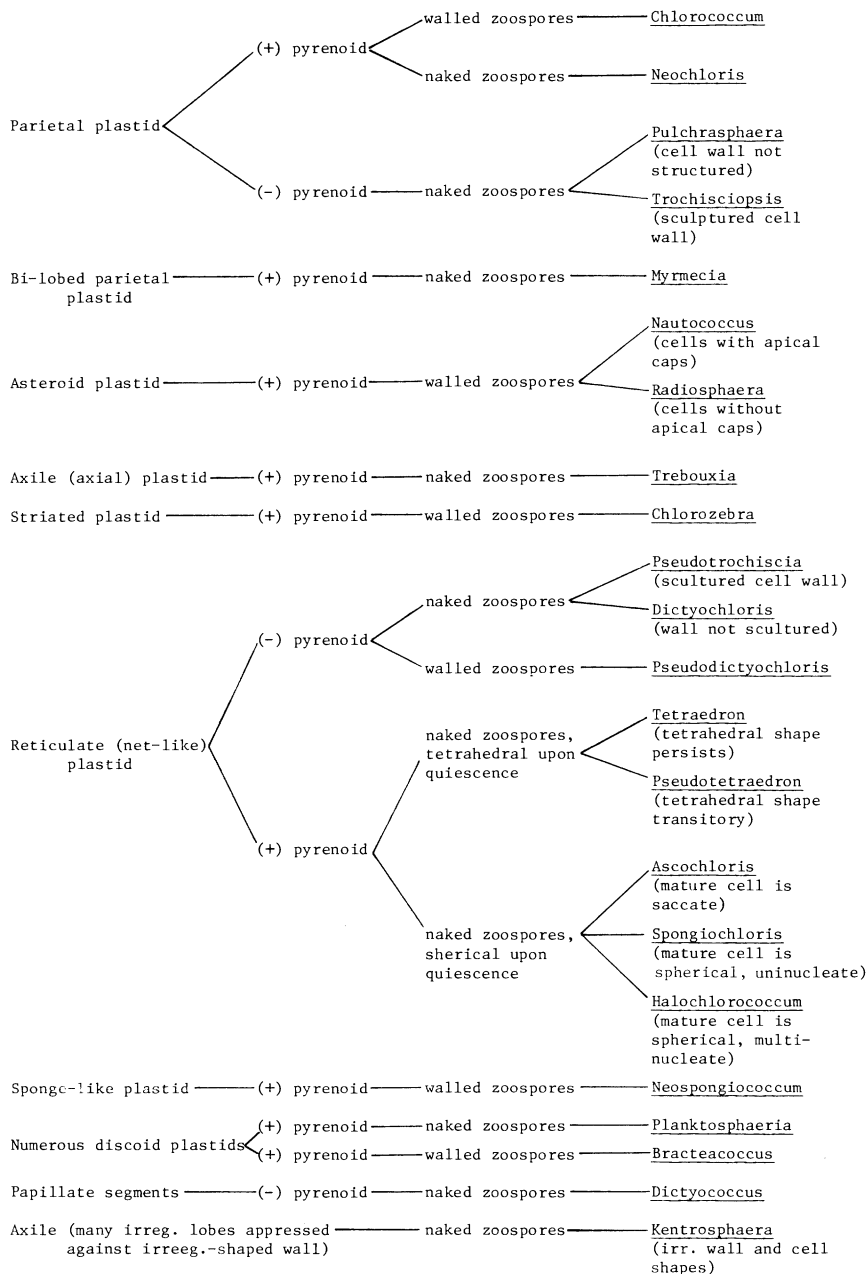


Fig. 3. Coccoid zoospore-producing soil algae.

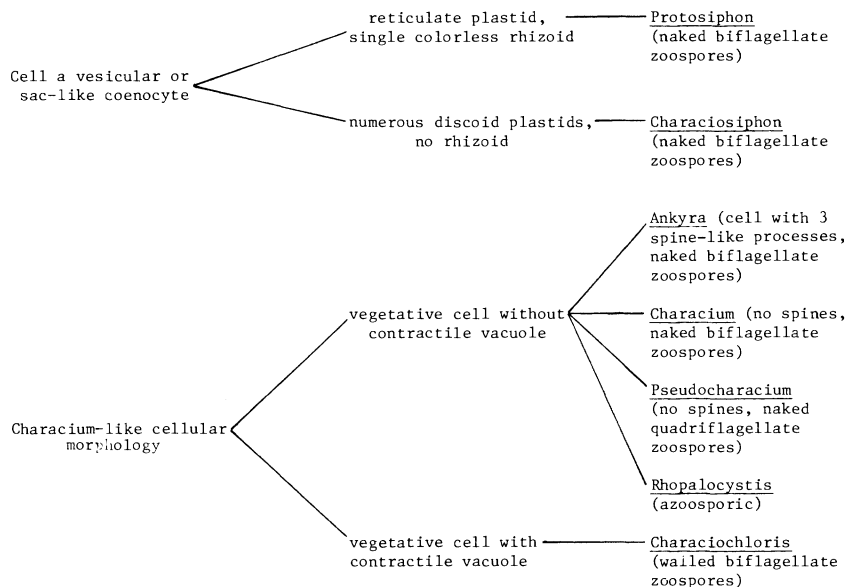


Fig. 4. Vesicular and *Characium*-like soil algae.

that a number of soil algae are facultative photoheterotrophs or chemoheterotrophs was first documented by Treboux (1905), while studies by Bristol-Roach (1926, 1927c, 1928a), Skinner and Gardner (1930), Ellner and Steers (1955), Samejima and Meyers (1958), Parker (1961), Parker et al. (1961), and more recently by Khoja and Whitton (1971), and Hoare et al. (1972) serve to demonstrate their widespread occurrence among higher taxa. The ability to utilize simple sugars and organic acids in the light or in the dark is deemed to be of taxonomic significance (Table I).

Most prokaryotic algae are facultative photoheterotrophs, although organic compounds seldom contribute significantly toward cell synthesis. Utilization of sugars by blue-green algae in culture seems to be restricted to glucose, fructose, and a few disaccharides (Stanier, 1973), while pyruvate and acetate can be incorporated into lipids and, to a lesser extent, into glutamic acid, proline, arginine, leucine, isoleucine, valine, and alanine (Hoare et al., 1972). Many diatoms are also photoheterotrophs or chemoheterotrophs in laboratory culture (Lewin, 1953). Table III summarizes much of the work by H. C. Bold and his students and co-workers. From it can be implied that perhaps 40–50% of green and yellow-green soil algae are facultative chemoheterotrophs. The tabulation includes those species for which growth in the dark was termed insignificant for systematic purposes, yet represents a potential for growth beneath the

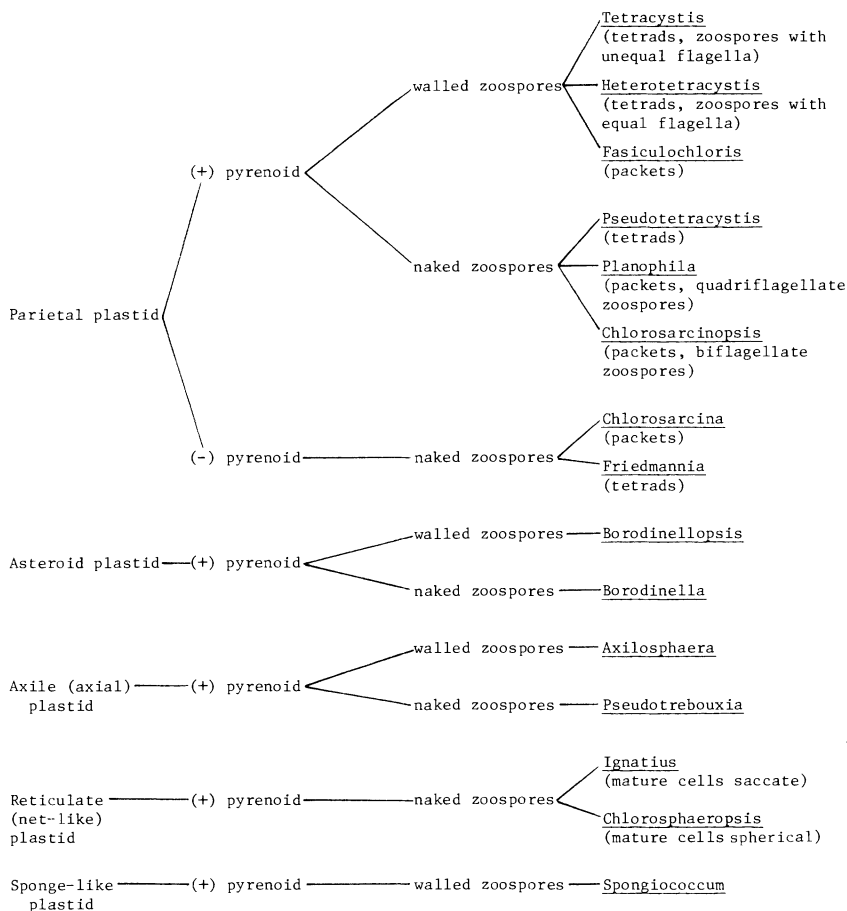


Fig. 5. Sarcinoid zoospore-producing soil algae.

soil surface. Compounds tested included acetate, pyruvate, fructose, glucose, ribose, and xylose, in addition to experimentation with other compounds, including media based on coconut milk (Cain, 1963).

A number of investigators have contended that the reason for predominance of diatoms and blue-green algae on alkaline soils is that there is often a greater availability of organic and inorganic nutrients (Fritsch, 1922a; Gistl, 1933; Petersen, 1935; John, 1942; Lund, 1945, 1947; Mitra, 1951). In laboratory experiments, growth and dinitrogen fixation by blue-green algae in Swedish soils was enhanced upon addition of inorganic nutrient solutions (Granhall and Henriksson, 1969). Concomitantly, predominance of green algae on and in acid soils may be due, in part, to the inability of other groups of algae to live at lower nutrient levels (Petersen,

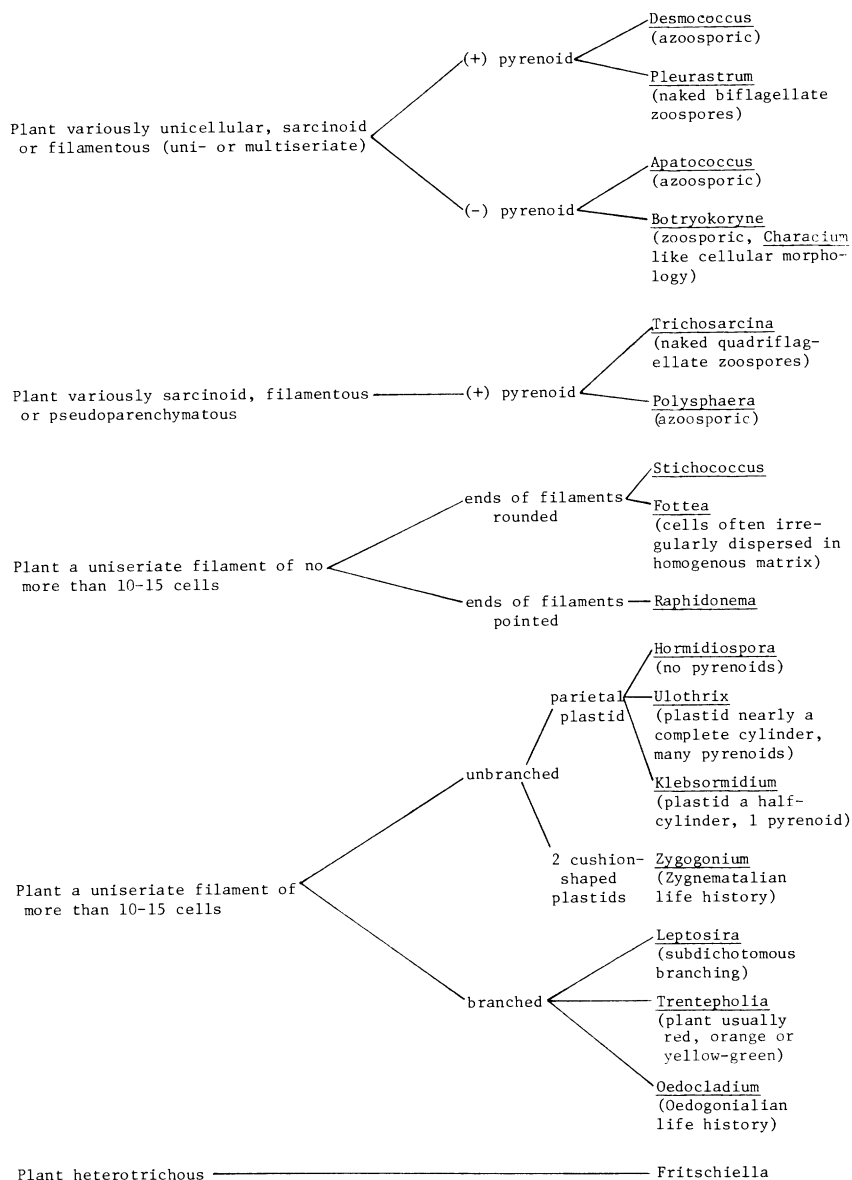


Fig. 6. Filamentous and pseudoparenchymatous green soil algae.

1935; John, 1942; Lund, 1947; Archibald, 1969). These conclusions are supported by experimental findings of Pringsheim (1950), who reported that diatoms will grow better in soil-water tubes with a relatively high volume ratio of soil to water. Soil high in organic matter, or enrichment

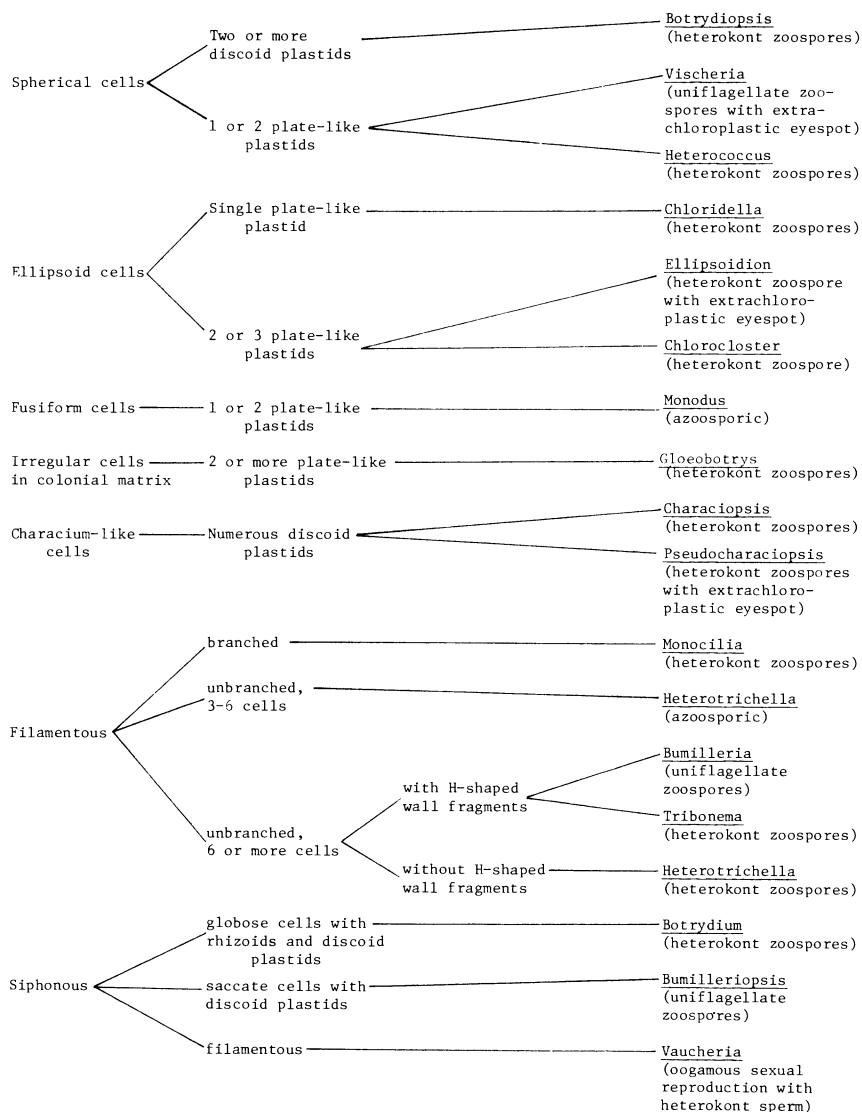


Fig. 7. Yellow-green soil algae.

media to which organic substances have been added enhance the growth of euglenoids from soil (Pringsheim, 1950). Whereas growth of algae in culture is usually limited by nitrogen, too much available phosphorus or nitrogen can suppress algal growth in the soil (Petersen, 1935; Lund, 1947). Fluctuating concentrations of nutrient ions in soil solutions probably act to stimulate or depress the activities of algae in soil through time (Hunt et al., 1979; Metting and Rayburn, 1979a; Metting, 1979).

Table III
Dark heterotrophic growth by soil algae in pure culture.

Genus	# Species exhibiting growth ^a	# Species without growth	Reference
<i>Ankyra</i>	1		Lee and Bold, 1974
<i>Asterococcus</i>		1	Cain, 1963; King, 1971
<i>Bracteacoccus</i>	5	1	Bischoff and Bold, 1963
<i>Characiochloris</i>	1		Lee and Bold, 1974
<i>Characiopsis</i>	1		Lee and Bold, 1974
<i>Characium</i>	10		Lee and Bold, 1974; Metting, 1980
<i>Chlamydomonas</i>	2	12	Bischoff and Bold, 1963; Cain, 1963; Cox, 1967; King, 1971
<i>Chlorella</i>	15	3	Shihira and Krauss, 1964; Karlander and Krauss, 1966
<i>Chlorococcum</i>	4	33	Archibald and Bold, 1970a; Metting, 1980
<i>Chloronomala</i>	1		Groover and Bold, 1969; King, 1971
<i>Chlorosarcina</i>	3		Groover and Bold, 1969
<i>Chlorosarcinopsis</i>	9	7	Chantanachat and Bold, 1962; Groover and Bold, 1969; Metting, 1980
<i>Cyanidium</i>	1		Doemel and Brock, 1971; Rigano et al., 1977
<i>Dictyococcus</i>	1		Metting, 1980
<i>Fasciculochloris</i>		1	Groover and Bold, 1969
<i>Friedmannia</i>	1		Groover and Bold, 1969
<i>Gloeotilopsis</i>		1	Deason, 1969;
<i>Heterochlamydomonas</i>		3	Langford and Cox, 1971
<i>Klebshormidium</i>	1		Deason, 1969
<i>Monodus</i>	1		Fogg and Miller, 1958
<i>Muriellopsis</i>	1		Cox, 1967, 1971 ^b
<i>Neochloris</i>	9		Chantanachat and Bold, 1962; Bischoff and Bold, 1963; Groover and Bold, 1969
<i>Neosporangiococcum</i>	3	23	Deason, 1976
<i>Oocystis</i>	1		Groover and Bold, 1969
<i>Ourococcus</i>	1		Bischoff and Bold, 1963
<i>Palmella</i>		1	Groover and Bold, 1969
<i>Palmellopsis</i>		1	King, 1971
<i>Planktosphaeria</i>	2		Bischoff and Bold, 1963
<i>Pleurastrum</i>	2		Groover and Bold, 1969; Metting, 1980

Table III
Continued.

Genus	# Species exhibiting growth ^a	# Species without growth	Reference
<i>Pseudochlorococcum</i>		2	Archibald, 1970
<i>Pseudogleocystis</i>		1	King, 1971
<i>Pseudotreboxia</i>	1		Archibald, 1977
<i>Radiosphaera</i>	3		Chantanachat and Bold, 1962; Cox, 1967
<i>Raphidionemopsis</i>		1	Deason, 1969
<i>Spongiochloris</i>	5	2	Chantanachat and Bold, 1962; Bischoff and Bold, 1963
<i>Tetracystis</i>	3	2	Chantanachat and Bold, 1962 ^c ; Bischoff and Bold, 1964 ^d ; Brown and Bold, 1964
<i>Tribonema</i>	1		Belcher and Fogg, 1958

^a Species of *Characium*, *Chlorosarcinopsis*, and *Tetracystis*, for which multiple strains were tested, showed dark heterotrophic ability to be species specific, although different strains of the same species often utilized different carbon compounds to variable extents.

^b *Muriellopsis* (Cox, 1971) was originally designated *Geosphaera* (Cox, 1967).

^c *Tetracystis diplobionticum*, originally described as *Chlorococcum diplobionticiuicum* by Chantanachat and Bold (1962), was emmended by Archibald and Bold (1970b).

^d *Tetracysits polymorphum*, originally described as *Chlorococcum polymorphum* by Bischoff and Bold (1963), was emmended by Archibald and Bold (1970b).

Whereas laboratory studies have shown that humic substances can stimulate growth of soil algae without acting as a direct nutrient source, the mode(s) of action is not known (Pratt, 1955; Lee and Bartlett, 1976). When compared with unamended plots of similar origin, soils supplied with farmyard manure have been observed to have both greater (Bristol-Roach, 1927a; Skinner, 1932b), and lesser (Petersen, 1935; Stokes, 1940a) numbers and kinds of algae. In extreme environments, greater algal diversity is encountered in microenvironments within which appreciable organic matter has collected (Cameron and Blank, 1966a; Boyd et al., 1970; Friedmann and Galun, 1974). However, in these instances it may be the indirect influence on moisture retention, and not the direct effect of organic materials which is important.

Whereas the moisture status of the soil may often determine whether the addition of inorganic nutrients stimulates or depresses algal activity in soil (Kaszubiak, 1976a; Comerton and Houghton, 1978), Gistl (1932, 1933) found that the addition of inorganic nutrients coincided with an increase in floristic diversity as compared with unamended soil. Seven-

teen species were encountered in soil to which kainite ($\text{KMg}(\text{SO}_4)\text{Cl} \cdot 3\text{H}_2\text{O}$) and $(\text{NH}_4)_2\text{SO}_4$ had been added. Superphosphate plus $(\text{NH}_4)_2\text{SO}_4$ were responsible for an increase to 20 species, kainite plus superphosphate increased the total to 27, and with all three dressings applied to the soil, 40 species of algae were found to grow. At concentrations of Cl^- , PO_4^{4-} , SO_4^{2-} , and SCN^- less than or equal to 0.01 M in laboratory culture, most soil algae were able to grow better than without the ions, or when the ions were supplied at higher concentrations (Gistl, 1933). Resident populations of soil algae have been used for the bioassay of calcium, phosphorus, nitrate, sulfate (Tchan, 1956, 1959; Tchan et al., 1961; Cullimore and Woodbine, 1963; Cullimore 1966a, 1966b, 1966c; Nekrasova and Burova, 1970), and potassium (Cullimore, 1965, 1967), in crop related tests, which indicates that, in general, algal activities in soil are probably dependent upon nutrient availability in much the same way as with vascular plants.

The extent to which excretion of enzymes by soil algae, first noted by Beijernick (1889), contributes to acquisition of nutrients is not known. Kaszubiak (1976b) reported that no correlation existed between numbers of soil algae and rates of mineralization. As with other physiological attributes, our knowledge of extracellular enzyme production is limited to an assessment of the degree to which the phenomenon is distributed among eukaryotic genera (Table IV). Of the extracellular enzymatic activities most frequently assayed, amylase appears to be widespread among species of soil algae, whereas gelatinase is not. Nitrataase activity has not been extensively examined in genera other than *Chlorococcum* (Archibald and Bold, 1970a) and *Neosporangiococcum* (Deason, 1976), within which it is uncommon not to possess the enzyme.

Many pedophycologists believe that most or all algal growth occurs by phototrophic assimilation of CO_2 within the upper millimeters (in fine soils), or centimeters (in coarse soils) of the soil profile, and that the subterranean flora includes only inactive, long-lived resting stages carried downward by water, agricultural activity, root growth, or the soil fauna (Petersen, 1935; John, 1942; Tchan and Whitehouse, 1953; Lund, 1962, 1967; Shields and Durrell, 1964; Gollerbakh and Shtina, 1969). These authors cite three facts as being predominantly responsible for reports of a subterranean algal flora. First, with few exceptions (Nordin and Blinn, 1972), have species of algae been isolated from below the surface of a soil which were not also found on the surface. Second, the large numbers of algae reported from beneath the level of the penetration of light might be accounted for by long term accumulation of resting stages of surface algae, which can remain viable for nearly a century (Bristol, 1919b; Lipman, 1941; Becquerel, 1942; Parker et al., 1969; Trainor, 1970). Third, it is often argued that heterotrophic growth of algae under laboratory con-

Table IV

Extracellular enzyme production by green and yellow-green soil algae in pure culture.

Genus	Amylase		Gelatinase		Nitrataase		Reference
	+	-	+	-	+	-	
<i>Ankyra</i>	1			1			Lee and Bold, 1974
<i>Asterococcus</i>	1			1			Cain, 1963; King, 1971
<i>Bracteacoccus</i>	6						Bischoff and Bold, 1963
<i>Characioclhoris</i>	1			1			Lee and Bold, 1974
<i>Characiopsis</i>	1		1				Lee and Bold, 1974
<i>Characium</i>	9			9			Lee and Bold, 1974
<i>Chlamydomonas</i>	8	5		2			Cain, 1963; Bischoff and Bold, 1963; King, 1971
<i>Chlorococcum</i>	30	7	19	18	31	6	Archibald and Bold, 1970a; Metting, 1980
<i>Chloronomala</i>	1			1			Groover and Bold, 1969; King, 1971
<i>Chlorosarcina</i>	2	1		3			Groover and Bold, 1969
<i>Chlorosarcinopsis</i>	14	2	6	10		1	Groover and Bold, 1969 ^{a,b} ; Metting, 1980
<i>Dictyococcus</i>		1		1		1	Metting, 1980
<i>Fasciculoclhoris</i>	1			1			Groover and Bold, 1969
<i>Friedmannia</i>	1			1			Groover and Bold, 1969
<i>Gloeotilopsis</i>	1			1			Deason, 1969
<i>Heterochlamydomonas</i>		3					Langford and Cox, 1971
<i>Klebsormidium</i>	2	2					Mattox and Bold, 1962 ^c ; Deason, 1969
<i>Muriellopsis</i>	1						Cox, 1967 ^d
<i>Neochloris</i>	2			1			Bischoff and Bold, 1963; Groover and Bold, 1969
<i>Neosporangiococcum</i>	21	4		25	22	3	Deason, 1976
<i>Oocystis</i>	1		1				Groover and Bold, 1969
<i>Ourococcus</i>	1						Bischoff and Bold, 1963
<i>Palmella</i>	1			1			Groover and Bold, 1969; King, 1971 ^e
<i>Palmellopsis</i>	1			1			King, 1971
<i>Planktosphaeria</i>	2						Bischoff and Bold, 1963
<i>Pleurastrum</i>	1	1		2		1	Groover and Bold, 1969; Metting, 1980
<i>Pseudochlorococcum</i>	2		2		1	1	Archibald, 1970
<i>Pseudogleocystis</i>	1			1			King, 1971
<i>Raphidionemopsis</i>	1			1			Deason, 1969
<i>Sporangioclhoris</i>	2						Bischoff and Bold, 1963
<i>Stichococcus</i>		3					Mattox and Bold, 1962
<i>Tetracystis</i>	11						Bischoff and Bold, 1963 ^f ; Brown and Bold, 1964

^a One of four strains of *C. pseudominor* Groover & Bold did not exhibit amylase activity.

^b For *C. dissociata* and *C. gelatinosa*, there were strains with and without amylase activity.

ditions does not mean that they would be able to compete successfully with saprophytic bacteria or fungi in the soil.

Evidence for microstratification of populations of algae within the upper millimeters or centimeters of soil profiles, gravel deposits, and rocks has been reported (Bristol-Roach, 1927a; John, 1942; Cameron and Blank, 1966a; Nordin and Blinn, 1972; Friedmann and Galun, 1974). Fritsch (1922b, 1936), and Flint (1958) termed yellow-green algae "shade forms" because they were often more abundant below the soil surface than on top. Contradictory evidence was presented by Petersen (1932), Lund (1945, 1947), and Willson and Forest (1957). Speculations based on consistent observations of high indirect counts led some to the conclusion that a level of algal activity exists at some distance (4–6") from the surface (Moore and Karrer, 1919; Moore and Carter, 1926; Bristol-Roach, 1927a; Fehér, 1936, 1948; Schwabe, 1960a, 1960b, 1963; Nordin and Blinn, 1972). This is supported by isolation of green (Bristol-Roach, 1927a) and blue-green (Vaidya, 1964) algae from depths greater than one meter. Kabirov and Minibaev (1976) presented evidence that the nanodistribution of algae on clods in wheat fields might be accounted for, in part, by variation in irradiance and moisture. They found yellow-green and green algae to be more abundant on east and west-facing surfaces than on south or north-facing surfaces.

Direct evidence for the existence of a metabolically active endeadaphic algal community was presented by Tchan and Whitehouse (1953), who, by observing chlorophyll fluorescence, showed that algae were present beneath the surface of two sandy soils, but that numbers of cells diminished rapidly below 4 millimeters. Penetration of light was dependent upon the water status of the soils, and was detectable to a depth of 2.9 centimeters, which correlated well with direct counts. Others have shown that light penetrates a small distance into coarse soils (Stewart, 1967a), and that distribution of algae is limited by this factor (Friedmann and Galun, 1974). While laboratory experiments suggest that the active downward movement of soil algae is unlikely (Petersen, 1935), displaced algae, once removed from light, probably remain active to an extent limited by substrate availability and microbial interaction.

SOLAR RADIATION

Spectral quality and photoperiod are important environmental factors controlling growth and differentiation of soil algae in the laboratory. Ex-

←
^c Only 1 of 17 strains of *K. flaccidum* (Kütz) Silva, Mattox & Blackwell exhibited amylase activity.

^d See footnote b, Table III.

^e Groover and Bold (1969) reported trace gelatinose activity, King (1971) reported no activity.

^f See footnotes c and d, Table III.

periments have shown that differentiation of heterocysts of *Nostoc muscorum* Ag. (Lazaroff and Vishniac, 1961), *Anabaena cylindrica* Lemm. (Fogg, 1951), *A. ambigua* (Kale, 1972), and *Camptylonema lahorens* Ghuse (Singh and Viswanathan, 1972) is light dependent. Heterocyst frequency is genetically fixed in *C. lahorens*, while photoperiod exerts some control over rates of differentiation (Singh and Viswanathan, 1972). Heterocyst frequency increased with lowered irradiance in *A. cylindrica* (Fogg, 1951). Wavelengths of 600–700 nanometers at 1300 lux resulted in greatest frequency of heterocyst differentiation in *A. ambigua* (Kale, 1972) and *A. doliolum* Bharadwaja (Tyagi and Ahluwalia, 1978). Differentiation of the plant mass of *N. muscorum*, and the completion of the sequence of morphological stages of its life history are also dependent upon wavelength and irradiance (Lazaroff, 1972). As will be discussed later, light plays an important role in regulating sex and zoosporegenesis in eukaryotic soil algae.

The geographic distribution of certain species of soil algae might be limited in northern latitudes by inadequate input of solar energy. In support of this hypothesis is laboratory evidence that nitrogenase activity in species of blue-green algae isolated from soils of northern Sweden does not light saturate up to 14,000 lux, coupled with the observation that maximum activity in the field takes place at noon on summer days (Granhall, 1975). Flint (1958), described the diurnal migration of a species of *Microcoleus* in sand on Louisiana beaches. He presented laboratory evidence that downward gliding was in response to increasing irradiance. In contrast, Kask (1976), found no correlation between irradiance and numbers of algae in soil.

The effects on soil algae of solar radiation in regions of the spectrum other than the visible have been documented to a limited extent. But (1962), Kumar (1963), and Cameron and Blank (1966b) have demonstrated that soil algae are, in general, more resistant to damage by ultraviolet radiation than are other soil microorganisms. Growth of *Stichococcus bacillaris* Nägeli was enhanced by a factor of four by sub-lethal doses of ultraviolet radiation (Chase, 1941). Fehér and Frank (1936, 1939, 1940) published evidence (questioned in print by Baatz, 1939) for the phototrophic utilization by soil algae of infrared and ultraviolet wavelengths. Chronic gamma irradiation of soil during the Brookhaven experiments revealed that prokaryotic soil algae are more resistant than eukaryotic species to these wavelengths (Franz and Woodwell, 1973). Pure culture studies with *Chlorella* sp. and *Chlamydomonas* sp. (Posner and Sparrow, 1964), and observations at the Nevada test site (Shields et al., 1961) and in Japan (Akiyama, 1966) support the conclusion that soil algae, although severely affected, are more tolerant of high energy radiation than are more complex life forms.

WATER

As dominant or co-dominant organisms in cold and hot deserts, and on aerial substrates in all latitudes on earth, soil algae, especially the blue-green algae, are well adapted for existence in climatic zones and local microenvironments in which available water is the primary limiting factor (Drouet, 1943, 1962a; Bolyshev, 1952; Moewus, 1953; Zehnder, 1953; Shields, 1957; Shields et al., 1957; Flint, 1960; Royzin, 1960; Cameron, 1960, 1961, 1962a, 1962b, 1963a, 1964b, 1966, 1969a, 1969b, 1970, 1971, 1972a, 1972b; Durrell, 1962; Friedmann, 1964, 1968, 1971, 1972; Cameron et al., 1965a, 1965b; Morelli et al., 1965; Cameron and Blank, 1965, 1966a; Cameron et al., 1966; Forest and Weston, 1966; Benoit and Cameron, 1967; Friedmann et al., 1967; Cameron et al., 1968; Cameron and Conrow, 1969a, 1969b; Gollerbakh and Shtina, 1969; Benoit and Hall, 1970; Cameron and Devaney, 1970; Cameron and King, 1970a, 1970b; Cameron et al., 1970; Novichkova-Ivanova, 1972a, 1972b; Friedmann and Galun, 1974; Friedmann and Ocampo-Paus, 1976).

The ability of soil algae to survive prolonged periods without water has been demonstrated by the successful revival of algae from stored soils and herbarium sheets up to 83 years of age. Circumstantial evidence that diatoms and yellow-green algae are less tolerant of low water potential includes their low abundance and diversity in soils of dry regions (Lund, 1945, 1947; Bredemühl, 1949; Friedmann and Galun, 1974), and their greater susceptibility to desiccation in laboratory tests (Bristol-Roach, 1928b; Skinner, 1932b).

Macrometeorological data do not present an accurate picture of moisture availability in soil microenvironments due to irregular temporal distribution of climatic events. On soil surfaces in temperate steppe (=semi-arid = semi-desert), and on and in rocks and soils in deserts, the only regularly available water is in the form of dew (Friedmann and Galun, 1974). Diurnal fluctuations in water status within microenvironments near the surface of the soil in moist temperate zones is also the result of nightly dew formation, and has been shown to coincide with fluctuations of algal populations within the space of 24 hours (Tchan and Whitehouse, 1953). Terrestrial algae, including edaphic species, are able to utilize gaseous water to maintain metabolic functions (Fritsch, 1922b, 1936; Friedmann and Galun, 1974; Turner, 1975; Favali et al., 1978) in much the same way as do lichens (Lange et al., 1970). Greening of takyr (place without plant) crusts within 15–30 minutes after a slight rainfall is a common phenomenon in Central Asia (Novichkova-Ivanova, 1972b) and the American southwest (Cameron and Blank, 1966a). Soil water potential has been shown to dictate the distribution of *Cyanidium caldarium* (Tilden) Geitler in a soil (Smith and Brock, 1973).

Xeric algal species must also be able to withstand extended periods when even atmospheric water vapor is unavailable. In addition to reports of the longevity of algae in stored soils and on herbarium sheets, it has been demonstrated that certain species of green and blue-green algae can survive temperatures exceeding 100°C when dormant in dry soil. A species of *Chlorella* was able to survive desiccation for one hour at 130°C (Trainor, 1962). Cameron et al. (1970), showed that species of blue-green algae, in soil, were able to survive five years of continuous high vacuum. Carson and Brown (1976) determined that altitude is not an important determinant in the distribution of genera of soil algae.

Experimental evidence for the physiological and biochemical mechanisms of drought resistance by terrestrial algae which do not form specialized resting cells is wanting. However, Fritsch (1916, 1922b), and others (Piercy, 1917; Fritsch and Haines, 1923; Fraymouth, 1928; Petersen, 1935; Evans, 1958, 1959; Shields and Durrell, 1964; Novichkova-Ivanova, 1972b) have suggested that extracellular mucilage (the algal sheath), the aggregation of cells and trichomes, intimate cytoplasm-cell wall contact, alteration of cell wall thickness and structure (evidenced by differential permeability to certain stains), absence of vacuoles, accumulation of refractive granules and oil droplets, viscous protoplasm, and altered pigmentation of sheaths and chromatophores are all responses to onset of drought and may be anatomical ramifications of physiological and biochemical adaptations for resistance to desiccation. Some of these phenomena may, however, be responses to stresses from insolation, and not moisture (Novichkova-Ivanova, 1972b; Friedmann and Galun, 1974).

In contrast to algae in perennially dry microenvironments are the majority of numbers and species, to which liquid water is available at relatively frequent intervals. In these situations, algal development is most pronounced at a moisture equivalent of from 40–60% of the soil's water holding capacity (Stokes, 1940a; Singh, 1942; Gollerbach and Shtina, 1969). Dinitrogen fixation by blue-green algae is optimal at 80–100% of the soil's water holding capacity (Tret'yakova, 1965; Shtina, 1972).

Adaptation by temperate and tropical soil algae, with respect to moisture stress, is not related as much to acquisition of water, as to the ability of algae to respond to the onset of dry periods by entering into a dormant or otherwise resistant state. Survival of sudden desiccation by populations of soil algae may be due to the fact that a certain number of individuals are retained in the resistant state at all times. Experimental work which has added to knowledge of the adaptive mechanisms by which soil algae survive dry periods has, in addition to the early work of Piercy (1917), Fritsch (1922b), and Fritsch and Haines (1923), come from studies of planktonic algae of ephemeral ponds (Lund, 1942; Evans, 1958, 1959). After studying the effects of rapid and gradual drying and rewetting of

pond margin litter and mud, Evans (1959), concluded that the longer the drying period, the longer the interval between initial rewetting and the production of metabolically active cells. He also suggested that sudden immersion in a relatively large volume of water might inhibit germination of resting stages. Also, more species survive slow drying than survive rapid desiccation, and, in addition to individual physiological responses to desiccation, certain algae may depend upon the death of peripheral individuals within a plant mass or coenobe to act as a protective barrier, thus ensuring survival of the population.

TEMPERATURE

Algal activity in soils in which moisture is not a limiting factor is governed, in large measure, by range and fluctuation of temperature. Algae are extremely resistant to low temperatures (Becquerel, 1936; Holm-Hansen, 1963a; James, 1955; Lund, 1962), with species of *Stichococcus* (Kärcher, 1931), *Microcoleus*, *Protococcus* (= *Desmococcus*), and *Schizothrix* (Cameron and Blank, 1966b) able to survive prolonged exposure to -192 to -195°C in crushed soil. Some species can slowly photosynthesize at -30°C in laboratory culture (James, 1955). Francé (1913), observed metabolizing individuals of *Nostoc*, *Cylindrospermum*, and *Hantzchia* in frozen soil.

Soil algae are better able to tolerate high temperatures under dry conditions (Glade, 1914; Izerott, 1937; Zehnder, 1953; DeMeter, 1956; Trainor, 1962), with growth of most eukaryotic forms in liquid media being inhibited in the 30 – 50°C range (Clendenning et al., 1956; Miller and Fogg, 1957). Limits of tolerance include 113°C for *Microcoleus vaginatus* (Vaucher) Gomont, 112°C for *Schizothrix* sp., and 110°C for *Scytonema ocellatum* (Booth, 1946). Trainor and McLean (1964) found that 100,000 cells of *Spongiochloris typica* Trainor & McLean per half gram of soil survived one year in air-dried soil followed by oven-drying for one hour at 100°C . The initial inoculum was of the order of 100 million cells per 20 grams of soil. Thermal resistance to less extreme temperatures, as indicated by $^{14}\text{CO}_2$ uptake rates, is different for green and blue-green algae. *Scenedesmus acutus* Hortobaggy exhibited a linear thermal death curve at 42, 45, and 47°C , while *Nostoc muscorum* and *Calothrix brevissima* G. S. West showed an initial period of insensitivity followed by an exponential death curve at the three temperatures (Venkataraman, 1964).

Although less has been written about the effects of fluctuating temperatures and moisture on soil algae, there is evidence that freeze-thaw cycles, and rates of temperature change are important variables (Höfler, 1951; Cameron and Blank, 1966b). Relatively high in situ Q_{10} values (4–6) for nitrogenase activity in antarctic blue-green algae (Fogg and Stewart, 1968), coupled with the fact that the temperature optimum for arctic

species is 15°C (Granhall, 1975), are evidence that soil algae adapt to temperature variation.

IONIC FACTORS AND PH

It is generally accepted that neutral and alkaline soils are more favorable to development of blue-green algae (Bolyshhev, 1952; Sdobnikova, 1956; Lund, 1962; Shields and Durrell, 1964; Cameron and Blank, 1966a; Fogg et al., 1973; Friedmann and Galun, 1974), although it must be kept in mind that these soils are usually dry and possess relatively high ionic strengths, and that these factors might be as important as pH. The distribution of blue-green algae in tundra soils is probably related, in a more direct way, to pH than in arid and steppe habitats (Alexander, 1975). In contrast, most acidic soils are dominated by communities of green and yellow-green algae (Petersen, 1915, 1935; Coyle, 1935; Flint, 1958; Lund, 1962; Shields and Durrell, 1964; Metting and Rayburn, 1979a). In only a few cases have opposite situations been reported, with blue-green algae being present in large proportion in acidic forest and nursery soils (Jurgensen and Davey, 1968), and green algae being dominant in an alkaline soil (Pulmaly, 1924). The conflicting reports of the preference by diatoms for high (Petersen, 1915, 1935; Lund, 1945; Flint, 1958), or low (Coyle, 1935) pH suggest that other factors, such as nutrient status (Lund, 1947, 1962; Shields and Durrell, 1964), in combination with pH are responsible for the distribution of this group of algae in soils. Liming of soils has been shown to increase both total numbers of algae, and the proportion of blue-green algae in the microflora (Stokes, 1940a; Balezina, 1975).

Numerous strains of blue-green algae (Durrell and Shields, 1961; Durrell, 1962; Koster, 1963), as well as *Chlorella vulgaris* Beijernick (Durrell, 1962), and *Porphyridium* sp. (Pringsheim and Pringsheim, 1956) are known to tolerate high ionic strengths. Gistl (1932) was able to show that a number of green, blue-green, and diatomaceous soil algae could survive in seawater for short periods of time. Algae in xeric habitats grow quite well in salt deposits, existing beneath the surface where desiccation and insolation are minimized (Cameron and Blank, 1966a; Friedmann and Galun, 1974). Laboratory studies with NaCl (Stewart et al., 1975), KCl, $(\text{NH}_4)_2\text{SO}_4$, and K_2SO_4 (Kennedy, 1970) suggest that the observation that algal dinitrogen fixation is inhibited by extracellular NO_3^- and NH_4^+ might, in part be a nonspecific effect of salt concentration. Field tests using independent additions of K_2SO_4 and MgSO_4 depressed dinitrogen fixation by blue-green algae in rice soils, a phenomenon not observed when the salts were added together (De and Sulaiman, 1950a).

OXIDATION-REDUCTION POTENTIAL

Low oxidation-reduction potentials associated with waterlogged soils are responsible, in part, for increased growth and dinitrogen fixation by

Table V

Numbers of species of green and yellow-green soil algae exhibiting growth in pure culture under microaerophilic conditions (in the light) or under anaerobic conditions (in the dark).

Genus	+	-	Reference
Growth	Growth		
<i>Ankyra</i>	1		Lee and Bold, 1974
<i>Asterococcus</i>	1		King, 1971
<i>Characiobchloris</i>		1	Lee and Bold, 1974
<i>Characiopsis</i>	1		Lee and Bold, 1974
<i>Characium</i>	10		Lee and Bold, 1974; Metting, 1980
<i>Chlamydomonas</i>	11		King, 1971
<i>Chlorococcum</i>	20	15	Archibald and Bold, 1970a; Metting, 1980
<i>Chloronomala</i>	1		Groover and Bold, 1969; King, 1971
<i>Chlorosarcina</i>	3		Groover and Bold, 1969
<i>Chlorosarcinopsis</i>	16		Groover and Bold, 1969; Metting, 1980
<i>Dictyococcus</i>	1		Metting, 1980
<i>Fasciculobchloris</i>	1		Groover and Bold, 1969
<i>Friedmannia</i>	1		Groover and Bold, 1969
<i>Neochloris</i>	1		Groover and Bold, 1969
<i>Neosporangiococcum</i>	17	8	Deason, 1976
<i>Oocystis</i>	1		Groover and Bold, 1969
<i>Palmella</i>	1		Groover and Bold, 1969; King, 1971 ^a
<i>Palmellopsis</i>	1		King, 1971
<i>Pleurastrum</i>	2		Groover and Bold, 1969; Metting, 1980
<i>Pseudochlorococcum</i>	2		Archibald, 1970

^a Groover and Bold (1969) reported microaerophilic growth of *Palmella texensis* Groover & Bold in the light in the presence of fructose, ribose, xylose and sodium pyruvate, while King (1971) reported growth only in media containing sodium pyruvate.

blue-green algae (Stewart and Pearson, 1970; Fogg et al., 1973). Activities of eukaryotic algae may be somewhat curtailed as potentials are lowered following a rainstorm (Tchan, 1953). In describing the physiological ecology of a perennial *Scytonema ocellatum* Lyngbye from grasslands in India, Singh (1942), determined that optimum growth took place at a moisture equivalent of 20–40% of the soil's water-holding capacity and an oxidation-reduction potential of –410 to –456 mv. Distribution among and within taxa of the ability to grow under microaerophilic and anaerobic conditions is best estimated from pure culture studies. About 75% of the green and yellow-green algae included in Table V show growth in una-

mended Bold's Basal Medium, or in the same medium supplemented with pentose or hexose sugars, or with an organic acid. At present, positive growth under anaerobic conditions has been demonstrated for five pal-melloid and chlamydomonad-like species from soil, as well as for all species of *Characium*, *Chlorosarcina*, *Chlorosarcinopsis*, and nine other genera. The species unable to grow belong to the genera *Chlorococcum*, *Neosporangiococcum* and *Characiochloris*.

SOIL TEXTURE

Although relationships have been observed between the micro-distribution of xeric algae on, under, and within rock, gravel, and diaphanous substrata (Shields and Durrell, 1964; Cameron and Blank, 1966a; Friedmann and Galun, 1974), little is known of the influence of soil texture on algal distribution. While the texture of mineral soils has been implicated as an important factor determining distribution of diatoms (Lund, 1945), and blue-green algae (Shields and Durrell, 1964), by virtue of its influence on infiltration and retention of water, Gonzalves and Gangla (1949b, 1949c) reported that the distribution of algae in soil sown to dry and irrigated wheat was not related to texture.

BIOTIC INTERACTIONS

A number of accounts of biotic symbioses which involve algae, including amensalism, competition, commensalism, proto-cooperation, parasitism, and neutralism have been reported (Parker, 1960). Most of the reports were based upon observations of planktonic associations or culture experiments which included soil algae. The best known symbiosis involving soil algae is that between dinitrogen-fixing blue-green algae, other microorganisms (Bjalfre, 1962; Perminova, 1964), and rice (Singh, 1961; Koptyeva and Tantsyuvenco, 1971). The work of M. B. Allen (1956a), in which she demonstrated that rice could grow in a nitrogen-free medium in association with blue-green algae, and of Stewart (1967b), and Mayland and McIntosh (1966a), who demonstrated that ^{15}N assimilated as N_2 by blue-green algae was transferred to higher plants, provided convincing proof that dinitrogen fixation by soil algae is a commensal activity.

A general picture of the influence of blue-green algae on resident populations of bacteria and fungi in soil is presented in Table VI, in which are summarized average plate counts for three major microbial groups from soil inoculated with dinitrogen-fixing algae, as compared with an uninoculated control.

Culture studies have demonstrated that soil algae excrete a variety of substances, including enzymes (see Table V, also Miller and Fogg, 1958), organic acids (Allen, 1956b; Taha and El-Refai, 1962a; Whitton, 1965;

Table VI

Changes in numbers of microorganisms ($10^6/\text{g}$) associated with algal-inoculation of soil as compared to fertilization (Venkataraman, 1966).

	Control	+ algae	+ $(\text{NH}_4)_2\text{SO}_4$	algae + $(\text{NH}_4)_2\text{SO}_4$
Actinomycetes	0.45	0.34	0.42	0.21
Bacteria	8.5	8.2	10.6	7.8
Fungi	0.035	0.025	0.088	0.021

Vaidya et al., 1970), polypeptides (Fogg, 1952; Chrost and Brzeska, 1978), nucleic acids (Singh, 1961), polysaccharides (Allen, 1956b; Lewin, 1956; Shnyukova, 1977), $\text{NH}_4\text{-N}$ and amide-N (Fogg, 1942, 1952; Fogg and Pattnaik, 1967; Stewart, 1963, 1977; Rzhanova, 1967), vitamins (Okuda and Yamaguchi, 1960; Brown et al., 1956) and other growth factors (Gupta and Shukla, 1964; Venkataraman and Neelakantan, 1967; Venkataraman, 1972), and antibiotics (Pratt, 1940; Pratt and Fong, 1940; Denffer, 1948; Emeis, 1956; Harder and Oppermann, 1953; Ruschmann, 1957, 1959).

The first definite report of an antibiotic substance from an alga was by Pratt (1940), who confirmed earlier speculation that algae produced products that inhibited growth of other algae and associated bacteria (Harder, 1917; Akehurst, 1931). The substance, chlorellin, was isolated from aged cultures of *Chlorella* sp., and found to be an unsaturated, long-chain fatty acid, inhibitory both to the alga itself and to various bacteria (Pratt and Fong, 1940; Spoehr et al., 1949). Accumulation of autoinhibitory organic peroxides in aged cultures of *Chlorella* has also been demonstrated (Scutt, 1964). Jorgensen (1956) and others (Harder and Opperman, 1953; Rice, 1954; Emeis, 1956) presented evidence that *Nitzschia palea* (Kütz.) W. Sm., *Chlorella pyrenoidosa* Chick, *Stichococcus bacillaris*, *Protophlon botryoides* (Kütz) Kelbs, and *Scenedesmus quadricauda* (Turp) Breb also excrete inhibitory compounds.

Mixed cultures of blue-green algae often exude bacteriostatic substances which can suppress root growth (Flint and Moreland, 1946; Flint, 1947; Jakob, 1954a, 1954b). Various aqueous and ethereal extracts of *Nostoc muscorum* have been shown to suppress *Cunninghamella* Matrchot damping off of millet in the laboratory (DeMule et al., 1977). In addition to studies with genera of hydroterrestrial algae, observations of phytoplankton interactions and results of culture work with aquatic and marine algae suggest the possibility that antibiotic production by algae in soil may be important (Lefevre et al., 1949; Lucas, 1949; McVeigh and Brown, 1954; Proctor, 1957a, 1957b). Antagonisms between edaphic blue-

green algae were reported by Srivastava (1972), who showed that *Anabaena* sp., a prolific spreader on agar, grew around *Hapalosiphon intricatus* W. & G. S. West leaving a clear zone around the plant mass of the heterotrichous alga. Observations of amensalism in culture with algae have, in some instances been unrelated to antibiotic activity. For example, concentration of CO₂ in streamwater, as influenced by the photosynthetic activity of *Stichococcus bacillaris*, was related to numbers of *Escherichia coli* (Migula) Castellani & Chalmers (Gray, 1975). Similar relationships could occur in soil solution. Oxygen production in rice paddies by blue-green algae antagonizes sulfate-reducing and other microaerophilic bacteria (Roger, 1973; Jacq and Roger, 1977), while stimulating root respiration of rice plants (Singh, 1961).

Studies using mixed cultures afford numerous examples of proto-cooperation among various members of the soil microflora in culture with algae. Proto-cooperation was observed in 2 of 21 alga-alga associations studied by Parker (1960), while a commensal relationship was noted for 3 of the 21 associations. A species of *Chlamydomonas* was shown to promote growth of a species of *Chlorella* in the laboratory (Allen, 1956b). *Chlorella vulgaris* is slightly antagonistic to *Scenedesmus quadricauda* in culture (Gel'fand et al., 1973). Forest et al. (1963), determined that there was no competition among *Nostoc muscorum*, *Ulothrix flaccida*, and *Scytonema hofmanni* Agardh in sterile soil.

Parker (1960), studied 122 additional two-membered associations involving soil algae utilizing media based on the Texas soil from which the microorganisms were isolated. He found that 53.1% of the combinations resulted in stimulation of the algal component, 14.7% resulted in inhibition, and 32.2% resulted in the alga being unaffected. Detailed investigations of 15 selected associations revealed that variations in irradiance, photoperiod, and temperature were not important, and that in most cases of proto-cooperation or commensalism, the association was between an autotroph and a heterotroph. In particular, *Bracteacoccus* sp. showed greater growth in association with an unidentified gram negative bacterium than in axenic culture because of a greater nitrogen supply resulting from the breakdown of complex organic compounds by the bacterium. Growth and motility of *Chlamydomonas* were enhanced in the presence of *Streptomyces* Waksman & Henrici sp. The increased motility of the alga was attributed to a decreased supply of nitrogen. Nitrogen depletion eventually resulted in increased production of akinetes by the alga, and of conidia by the actinomycete. Growth of *Phormidium* was inhibited by an unknown factor in the presence of an unidentified fungus (Parker, 1960; Parker and Bold, 1961).

Parker and Turner (1961) calculated a community interaction value (CI) for any pair of soil algae. A measure of the similarity of the theoretical

niche requirement of two algae, the CI was set equal to the fraction of the total number of comparable microbial associations in which dissimilar associative effects were noted. The closer to zero the CI for any two algae, the more nearly similar is their niche requirement.

Perhaps the best documented biotic interaction between soil algae and other free-living microorganisms includes one or another strain of *Azotobacter* Beijernick. Species of *Azotobacter* (as well as of *Bacillus* Cohn and *Clostridium* Prazmousski) have been isolated from extracellular mucilages of *Nostoc* sp., *Gloeocapsa* sp., and *Rivularia* sp. (Roth) Agardh (Jones, 1930). Nearly twice as much total nitrogen was recovered from tapwater cultures of *Chlorella* and *Azotobacter*, than from cultures of the bacterium alone (Lipman and Teakle, 1925). Nakano (1917) claimed that green algae stimulated growth of *Azotobacter*, while Stokes (1940b) reported a commensal effect. While able to utilize nitrogen fixed by *Azotobacter* sp., carbon from *Microcystis* Lemm. sp. (isolated from fresh-water) was unavailable to the bacterium (Skoog and Gerloff, 1955). Growth of blue-green algae in rice paddies might be responsible for the poor development of populations of *Azotobacter* (Sulaiman, 1944). Green and blue-green algae have also been employed in attempts to isolate and replicate species of *Rhizobium* Frank by means of artificial symbiosis (Korinek, 1953).

In other studies, an unidentified heterotrophic bacterium in association with *Chlamydomonas* sp., resulted in a seven-fold increase in growth of the alga when a soil dialyzate was used as the base for the medium (McVeigh and Brown, 1954). Studies with *Chlorella* sp. revealed that photosynthetic oxygen production stimulated growth of *Streptomyces* sp. and that alcohol production by the actinomycete inhibited the alga (Ruschmann, 1957). A protocoperative association was noted between *Chlorella* sp. and *Corynebacterium* Lehmann & Neumann in the same set of studies (Ruschmann, 1957). Trainor (1963) showed that *Scenedesmus dimorphus* Kutz, which forms coenobes in pure culture, is unicellular when grown in association with a heterotrophic soil bacterium.

Soil algae serve as sources of energy for protozoa (Old and Darbyshire, 1978), nematodes (Tchan and Whitehouse, 1953), snails (Comerton and Houghton, 1975), microarthropods (Broadhead, 1958; Wheeler et al., 1972; Gerson, 1976a, 1976b), and earthworms, whose gut contents were found to include *Calothrix*, *Phormidium*, *Cylindrospermum*, *Pinnularia*, and *Navicula* (Atlavinyte and Pociene, 1974). Algae are readily decomposed by bacteria and fungi upon death. Watanabe and Kiyohara (1960) noted that decomposition rates varied among species of bacteria, including *Achromobacter* (= *Alcaligenes* Castellani & Calmers), *Bacillus*, *Flavobacterium* Bergey, and *Pseudomonas* Migula. Upon death of the algae, whole cells, cell walls, cytoplasm, and extracellular polysaccharides

served as energy sources for saprophytic microorganisms in the soil. Species of *Anacystis*, *Microcoleus*, *Plectonema*, and *Stichococcus*, isolated from a sandy loam, and of *Anabaena flos-aquae* (Lyngb.) Breb, *Nostoc muscorum*, and *Chlorella pyrenoidosa*, isolated from other habitats were readily decomposed after 22 weeks incubation in soil in the laboratory. Sixty-one to 81% of the radioactive carbon originally incorporated into the various cellular and extracellular components during pretreatments was evolved as $^{14}\text{CO}_2$. Complexing of walls and cytoplasmic preparations from *A. flos-aquae* and *N. muscorum* with model humic acid-type phenolic polymers reduced decomposition of these structures (Verma and Martin, 1976).

Little is known of the systematic affiliations of the bacteria that inhabit the cell surfaces and extracellular sheaths of soil algae. Among 170 strains of blue-green algae studied by Shtina (1968), the nonspore-forming gram negative bacteria predominated. Upon aging of cultures, she found the bacterial community to become less complex, with only *Pseudomonas radiobacter* (= *Agrobacterium radiobacter* Beijernick & van Deldea), *Flavobacterium* sp., and *Caulobacter* sp. Henrici & Johnson remaining after three months. The difficulty with which blue-green algae are separated from bacteria reflects their close association. While most mucilaginous sheaths harbor a variety of satellite bacteria, especially species of actinomycetes, *Caulobacter*, *Chromobacterium* Bergonzini, and *Pseudomonas* (Gromov, 1964; Bershova et al., 1968; Sokolova, 1971), their interrelationships are not well understood. The lichen, whether a parasitic, commensal, or protocoperative symbiosis, is perhaps the most well understood biotic interaction involving terrestrial algae. It is beyond the scope of this review to consider the systematics or ecology of lichens. Suffice it to say that in many circumstances there seem to be no great ecological dissimilarities between lichens and algae.

LIFE HISTORIES

Little or no information is available on the environmental regulation of algal life histories in soil. Aside from empirical observations that seasonal fluctuations in soil moisture and temperature are primarily responsible for algae entering into, and germinating from dormancy, no other information concerning the influence of the environment on development, differentiation, or sexual reproduction in soil has been reported.

Perhaps the best description of an in situ response to an environmental trigger is that of Cameron and Blank (1966a), who recorded the events associated with zoosporogenesis and production of hormogonia by algae in desert rain crusts. Epedaphic communities in deserts exist as rain crusts, algal crusts, or lichen crusts (Cameron and Blank, 1966a). The

physiognomy of these synusia is described below in the section on community ecology. Rain crusts are microephemeral communities that are easily displaced into microdepressions by rainwater. In response to the disruptive action of raindrops and the subsequent horizontal movement of surface water, the desiccated algal sheaths soften and swell. Then the trichomes migrate to the sheath boundary and are explosively propelled into the surrounding water where cell divisions (including zoosporogenesis in eukaryotic forms) allow the algae to complete their life histories before the micropools dry up (Cameron and Blank, 1966a).

Because there are no accounts of sexual or parasexual processes by soil algae in situ, the only clues as to the probability of their occurrence and the microenvironmental conditions which promote differentiation are garnered from laboratory observation and experimentation. The work of Lazaroff and Vishniac (Lazaroff, 1955, 1966, 1969, 1972; Lazaroff and Vishniac, 1961, 1962, 1964), concerning the developmental cycle of *Nostoc muscorum* in pure culture, has suggested that light and nutrition play prominent roles in controlling the growth and reproduction of blue-green algae in soil. Growth in the dark and in media containing sugars favors the development of packets of coccoid cells (Lazaroff and Vishniac, 1961). Light is required for the development of trichomes and hormogonia, although the response is not associated with the photosynthetic machinery. Induction of trichome development is related to spectral quality, with 650 nanometers optimizing trichome formation. Photoreversal of red-induced development is accomplished with 450–480 nanometers (Lazaroff, 1966). Hormogonial swarming by *N. muscorum*, in pure culture, is also related to irradiance, but is a photosynthetic-dependent, energy-related response, and may be enhanced by photoassimilation of monosaccharides. Duration of motility of hormogonia is also a photokinetic response (Lazaroff, 1969, 1972).

To species of eukaryotic soil algae, nutrition plays an important role in the differentiation of motile cells in culture. Nutrition and light are the key to zoosporogenesis in *Protosiphon botryoides* Klebs. Nitrogen, sulfur, or calcium deficiency, in culture, decreased the incidence of zoospore production and release, while stimulation was noted upon addition of nitrate in the absence, but not in the presence of calcium and sulfur (O'Kelley and Herndon, 1961; O'Kelley and Deason, 1962). Zoospore production by *P. botryoides* is rare below pH 3.6, or above pH 9.2 (Maher, 1947), but is virtually unaffected between pH 5.1 and 7.7 (O'Kelley and Deason, 1962). Osmotic pressure does not affect zoosporogenesis (O'Kelley and Deason, 1962).

Of the numerous algae which have been isolated from soil, few have been observed to undergo sexual differentiation or gametic union in the soil or in the laboratory. The process has been observed, to an apprecia-

ble extent, in only four genera, *Chlamydomonas*, *Heterochlamydomonas*, *Tetracystis*, and *Oedocladium*. None of the edaphic species in at least 30 genera, that are known to produce motile asexual cells, have ever been observed to produce gametes. In all likelihood, an appreciable number of these species are able to differentiate given the appropriate set of environmental circumstances in the soil. The fact that Archibald and Bold (1970a) were unable to elicit a sexual response from cultural descendents of *Chlorococcum minutum* Starr or *C. diplobionticum* Herndon, species for which gametic union had previously been described (Starr, 1955; Herndon, 1958a), tends to substantiate the preceding speculation.

The hypothesis that nutritional factors act as primary regulatory agents of cellular, thalloid, and sexual differentiation by algae in soil can be argued for on the basis of a number of substantiated phenomena pertaining to species isolated from aquatic habitats. Sager and Granick (1954), were the first to report that nitrogen depletion in laboratory culture controlled the sexual response of an aquatic strain of *Chlamydomonas reinhardtii* Dang. The response was obviated in the dark, and it is now known that an adequate supply of CO₂ and proper conditions of illumination are also necessary for sexual differentiation in a number of species of *Chlamydomonas* (Tsubo, 1956; Trainor, 1958, 1959; Bold and Wynne, 1978). Nutrient depletion is also the primary trigger in species of *Cylindrocystis* (Biehel and Chamberlin, 1970), *Golenkinia*, Chodat (Ellis and Machlis, 1968), *Oedogonium* (Hill and Machlis, 1970), *Pandorina* Bory (Wilbois, 1958; Rayburn and Starr, 1974) and *Scenedesmus* (Trainor and Burg, 1965). Sulfur deficiency was as effective as nitrogen in evoking sexual differentiation in *Pandorina unicocca* Rayburn and Starr (Rayburn and Starr, 1974), while phosphorus was nearly as effective as nitrogen for *Golenkinia* sp. (Ellis and Machlis, 1968).

Nutrition has also been shown to regulate zoospore formation in various yellow-green algae (Pecora and Rhodes, 1973), and zoospore and resting spore formation in *Protosiphon* (O'Kelley and Herndon, 1961; Berkaloff, 1975). Nutritional factors probably contribute to cellular differentiation by soil diatoms as well. Although responses vary with temperature and irradiance (Drebes, 1966; Werner, 1971), auxospore formation is triggered by phosphate depletion in certain marine species (Drebes, 1966), as is gametogenesis in other species by manganese depletion (Steele, 1965). In yet other marine diatoms, an increased rate of sexual differentiation is linked to increasing concentrations of sodium (Schultz and Trainor, 1968).

Of the myriad of factors which might regulate algal life histories in soil, only pH has been shown not to influence differentiation of motile cells in species of *Bracteacoccus*, *Chlorococcum*, and *Neochloris* (Hancock, 1960). Temperatures from 3 to 22°C, were not shown to greatly in-

fluence zoospore production by *Tetraspora gelatinosa* Kützing (Rhodes and Herndon, 1967).

ALGAL COMMUNITY ECOLOGY IN SOIL

ROLE IN COMMUNITY SUCCESSION

The activities of algae contribute both to the formation of soils and to the integrity of mature soils. Algae constitute the initial synusium on substrates recently exposed to the biosphere, including volcanic deposits and bedrock (Treub, 1888; McLean, 1919; Shields et al., 1957; Singh, 1961; Morelli et al., 1965; Cameron and Benoit, 1970; Schwabe, 1972; Brock, 1973). The kinds of algae that act as primary colonizers depends largely on chance dispersal. Treub (1888) reported that the first colonists on recent deposits from the Indonesian volcano Krakatoa were blue-green algae of the genera *Anabaena*, *Lyngbya*, *Symploca*, and *Tolypothrix*. Following the volcanic creation of Surtsey, off of the coast of Iceland, Schwabe (1972) identified over 100 species of algae, including about 10% blue-greens, while others (Brock, 1973; Rodgers and Henriksson, 1976) found moss protonema, lichens, and coccoid green algae, a phenomenon repeated on Katmai (Alaska). Apparently Krakatoa was colonized by blue-green algae because they were the most abundant forms on land-forms closest to the new island, whereas green algae, lichens, and mosses predominate on Iceland and in the Aleutians. The speed with which these volcanic islands were colonized is not surprising in light of the fact that air currents are known to act as a constant source of algal propagules (Schlichting, 1961, 1964, 1969, 1974; Brown et al., 1964; Brown 1969). Discoloration of roofs further attests to the airborne tendencies of algae (Brooks, 1968).

On primary substrates, algae promote the weathering of silicate minerals by aiding the retention of water, which is the primary weathering agent, and by creating slightly acidic conditions by the photosynthetically-induced production of carbonic acid (Diels, 19; Ercegovic, 1925; Glazovskaya, 1950; Bolyshev, 1952, 1968; Gromov, 1957; Royzin, 1960; Friedmann, 1972; Folk et al., 1973; Marathe and Chaudhari, 1975). Aristovskaya et al. (1969), concluded that the actions of extracellular polysaccharides of algae were among the most important microbiological processes promoting the release of nutrient elements from insoluble compounds while Smith et al. (1978), provided laboratory evidence that algae extract orthophosphate from naturally-occurring apatite. Growth of diatoms has been implicated in the breakdown of kaolin (Vinogradov and Boychenko, 1942). The actions of cliff-dwelling algae have been reported to be responsible, by virtue of dinitrogen fixation and release of chemical elements from rock, for the fertility of mountain valley soils (Krasil'nikov, 1949, 1956). Odintsova (1941) suggested that nitrate deposits

in Western Pamir were the result of long-term accumulation of nitrogen fixed by chasmolithic blue-green algae.

The floristic makeup of algal communities on and in rocks appears to be dependent on moisture, insolation, and the nature of the substrate (Singh, 1961; Shields and Durrell, 1964; Friedmann and Galun, 1974). In moist temperate regions, limestone is often colonized by species of *Scytonema*, which can grow into the fabric of the rock to a depth of 8 mm (Diels, 1914). Other rock surfaces, especially smooth ones, may be colonized by blue-green algae of the genera *Aphanocapsa*, *Gloeocapsa*, *Gloeotheca*, *Nostoc* (Fritsch, 1907a, 1922a), and *Scytonema* (Singh, 1961). More acid rock surfaces in moist temperate zones support growth of filamentous green and blue-green algae, and of moss protonema (Fritsch, 1922a). When shaded, siliceous and calcareous rock often support *Tolypothrix byssoidea* (Mass.) Kirchn., *Stigonema minutum* (Ag.) Hassal, and species of *Gloeocapsa*, which can weaken the integrity of the rock to the point where it is easily peeled off, by hand, to a depth of 1–2 mm (Ercegovic, 1925; Fritsch, 1936).

In arid regions extremes of moisture, insolation, and temperature may prohibit succession from advancing beyond primary colonization by cryptogams (Cameron and Blank, 1966a; Friedmann and Galun, 1974). Different groups of algal species predominate in chasmolithic, epilithic, epedaphic, and enedaphic microenvironments forming the climax community (Shields et al., 1957; Cameron and Blank, 1966a; Friedmann, 1972; Friedmann and Galun, 1974). Epedaphic communities exist as rain crusts, algal crusts, or lichen crusts (Cameron and Blank, 1966a). An algal crust is defined as a visible, adherent plant mass, in contrast to the mobile, microephemeral nature of the rain crust. Algal crusts are common in steppe and desert zones throughout the earth's latitudes (Drouet, 1943; Bolyshev and Evdokimova, 1944; Bolyshev and Manucharova, 1947; Bolyshev, 1952, 1955, 1968; Moewus, 1953; Sdobnikova, 1956; Shields et al., 1957; Cameron, 1961, 1962a, 1963a, 1963b, 1964a, 1964b; Friedmann, 1964; Cameron and Blank, 1966a; Friedmann et al., 1967; Cameron and Devaney, 1970; Friedmann and Galun, 1974). According to Cameron and Blank (1966a), who adhere to the conservative classification of Drouet (1962b, 1963, 1964, 1968, 1973; Drouet and Daily, 1956), the most common constituents of algal crusts around the world are *Anacystis mariana* (Lightfoot) Drouet & Daily, *A. montana* (Hansg.) Drouet & Daily, *Coccochloris stagnina* [= *Aphanotheca stagnina* (Spreng.)], *Nostoc muscorum*, *Scytonema hofmanii*, *Porphyrosiphon fuscus* Gomont, *Microcoleus vaginatus* (Vaucher) Gomont, *M. chthonoplastes* (Mert.) Zanard, *M. paludosus* (Kützing) Gomont, *Palmogoea protuberans* (Sm. & Sow.) Kützing, *Protococcus grevillei* (Agardh) Crouan, *Protosiphon botryoides*, *Chlorella vulgaris*, and *Trochisia hirta* (Reinsch) Hansg. Bolyshev (1952),

who follows the traditional classification of blue-green and green algae, listed the following genera (with numbers of species in parentheses) as the most important in takyr (algal) crusts: *Phormidium* (10), *Lyngbya* (9), *Nostoc* (4), *Oscillatoria* (2), *Microcoleus* (2), and one species each of *Aphanothece*, *Chlamydomonas*, *Chlorella*, *Chorococcum*, *Calothrix*, *Hantzchia*, *Navicula*, *Nodularia*, *Palmella*, *Protococcus*, *Scenedesmus* and *Schizothrix*. Forest (1965) reported that two takyr crust samples included *Symploca atlantica* Gomont, *Schizothrix calcicola*, and *Microcoleus cthonoplastes*. *Nostoc* spp. also form algal crusts along sandy shores on Sri Lanka (Fritsch, 1907b). Desert varnish, an irregularly-distributed dark brown or black-colored surface coating up to 1 mm thick in arid regions, may result from the actions of algal metabolites which chelate iron and manganese in and around algal and rain crusts (Krumbein, 1969; Bromfield, 1976).

Lichen crusts are ecological equivalents of algal crusts and have been regarded as the climatic climax in desert microenvironments, superceding algal crusts following invasion by fungi (Cameron and Blank, 1966a). However, Killian (1953) reported that algae in the Sahara were never lichenized. Takyr crusts often become lichenized through a sequence that includes invasion of the periphery followed by growth along major cracks in the algal crust, and finally, complete conversion of the thallus into a lichen (Bolyshhev, 1955).

Chasmolithic communities in flint and plutonic rocks, and all endolithic microenvironments in Middle Eastern deserts are dominated by *Gloeocapsa* sp., while sarcinoid green and filamentous blue-green algae dominate in dolomitic and calcareous substrates (Friedmann, 1968, 1972; Friedmann and Galun, 1974; Friedmann and Ocampo-Paus, 1976).

Diaphanous materials (quartz, chalcedony, dolomite, bone or shell fragments) embedded in the surface of desert soils create microgreenhouses through decreased insolation, increased moisture retention, and moderated temperature extremes (Durrel, 1956; Kers, 1976; Berner and Evenari, 1978). These special conditions promote the development of a more diverse microflora than do other desert microenvironments. Friedmann and Galun (1974) reported that the enedaphic algal flora associated with diaphanous substrata in the Negev (Israel) was comprised of the following "fensterflanzen" [Vogel (1955) applied the term *fensterflanzen* (window plants) to highly evolved angiosperms (Aizoaceae and Liliaceae), whose leaf anatomy created a situation analogous to that of a diaphanous material.]: *Bracteacoccus* sp., *Chlorosarcinopsis* sp., *Stichococcus* sp., *Trochisia* sp., *Trebouxia* sp. (as a lichen component), *Friedmannia israelensis* Chantanachat & Bold, *Klebsormidium sterile* (Deason & Bold) Silva, Mattox & Blackwell, *K. subtilissima* (Mattox & Bold) Silva, Mattox & Blackwell, and *Radiosphaera negevensis* Ocampo-Paus

& Friedmann in various associations with species of *Aphanocapsa*, *Aphanothece*, *Gloeocapsa*, *Lyngbya*, *Nostoc*, *Plectonema*, *Scytonema*, *Microcoleus*, *Schizothrix calcicola* and *Tolypothrix byssoidea* (Mass.) Kirchner. They also reported *Scytonema ocellatum* from Egypt. Durrell (1962), listed *Tolypothrix distorta* Kützing, *Nostoc muscorum*, *Microcoleus vaginatus*, *Anacystis montana*, three species of *Phormidium*, and *Chlorella vulgaris* as occurring beneath diaphanous materials in Death Valley, California. *Phormidium tenue* (Meneg.) Gomont grew under salt crusts (Durrell, 1962), while Shields et al. (1957), found *Palmogloea protuberans*, *Plectonema nostocorum* Bornét, and rarely, *Microcoleus vaginatus*, *M. paludosus*, *Schizothrix hofmanii*, or *Nostoc* spp. beneath gypsum crusts.

In secondary community succession, algal growth is an important avenue for the input of organic carbon and nitrogen. Accumulation of humus is important for moisture retention and for the establishment of a seedbed (West and West, 1897; Fritsch and Salisbury, 1915; Fletcher and Martin, 1948; Aleksandrova, 1951; Bolyshev, 1952, 1955, 1968; Gollerbach, 1953; Singh, 1961; Mayland et al., 1966; Bolyshev and Novichkova-Ivanova, 1978).

It has been shown that germination of broadcast sown grass seed can be decreased by mature algal crusts as compared with bare soil, however, once established, seedlings grow more rapidly in the presence of algae (McIlvanie, 1942). In secondary succession, algae help establish stabile soil structure through aggregation of colloids by means of extracellular polysaccharides, including filamentous sheaths and individual and colonial mucilages (Martin and Waksman, 1940; Fletcher and Martin, 1948; Singh, 1961; Bond and Harris, 1964; Marathe, 1970; Anatani and Marathe, 1972a, 1972b; Bailey et al., 1973; Venkataraman, 1975; MacKenzie and Pearson, 1979). Aggregation of soil particles helps to improve infiltration and percolation of water thereby reducing erosion (Elwell et al., 1939; Booth, 1941a, 1941b; Fletcher and Martin, 1948; Singh, 1961). Soil samples from eroded farmland in Oklahoma averaged 8.9% water when covered by algal growth, as compared with 1.3% water when bare (Booth, 1941a). Within the upper inch of samples from India, bare soil contained 10–15% less water than when supporting growth of algae (Singh, 1961).

Experimental evidence supports the hypothesis that there are no algal species which operate specifically as pioneer algae in secondary succession (Forest et al., 1959). There are instances however, when seasonal variations within algal communities take place in response to agricultural disturbances and other human activities. The best known examples are annual successions within flooded paddy soils (Ciferri, 1960; Singh, 1961), and successions associated with reclamation of sodic-saline ("Usar") soils in India (Singh, 1950, 1961), to be discussed later. In Brazil, large

tracts of land become covered by *Porphyrosiphon notarisii* Kützing (Drouet, 1937), while in India, extensive wefts of the same species are commonly found as co-dominants in grasslands and on otherwise bare soils, imparting a crimson or brick-red hue. Yellow-brown, jelly-like masses of *Nostoc commune*, dark blue-green patches of *Cylindrospermum* sp., shiny dark-brown patches of *Scytonema ocellatum*, and variously hued growths of *N. muscorum*, *N. humifusum* Carm. ex Bornet & Flahault, and *Aulosira fertilissima* Rao on fallow fields are also seasonal dominants in India (Singh, 1961).

In England, *Klebsormidium flaccidum* (A. Brown) Silva, Mattox & Blackwell, exists in dry grasslands as a codominant, becoming dominant during the first year or two following a major drought which may kill much of the vascular vegetation (Piercy, 1917). On burned heath, green algae were the first plants to become established, followed by mosses and forbs (Fritsch and Salisbury, 1915). The only evidence of seasonal succession within algal communities of undisturbed soils was provided by Fehér (1936, 1948), who reported that in central Europe, green algae were succeeded in the summer by blue-green algae in conifer woods, and that in dicot woods, the reverse was true. In northern Europe, according to Fehér, the opposite situation prevailed with respect to which algal groups predominated in relation to season and macrovegetation.

STRUCTURE OF ALGAL COMMUNITIES

The structure of microbial communities in soil is defined on the basis of biomass and diversity, and changes in these properties over time. There have been numerous compilations of floristic lists of soil algae, but because of inconsistencies in taxonomy of green and blue-green algae, meaningful comparisons of these lists, especially of lists older than about 1955, are limited.

Biomass determinations of soil algal communities are wanting. Estimations have been made, based on an average volume of an algal cell (Fehér, 1936), but the only reliable basis, at present, for estimating this important parameter is assessment of numbers of algae in a known mass of soil. Again, a direct comparison of numbers reported by one individual with those by others is difficult. This is because a variety of counting methods and enrichment media have been used and investigators disagree as to what the basic algal unit should be. Also, the manner and extent to which counts are extrapolated and averaged (Forest, 1962; Nekrasova and Busygina, 1977; Kabirov, 1978; Roger and Reynaud, 1978), and the degree of dispersal of the soil during dilution procedures (Petersen, 1935) have been shown to contribute to variation among estimates. For example, direct and indirect counts have been shown to differ by as much as 44% (Tchan and Whitehouse, 1953), and floristic estimates of com-

munities vary when more than one enrichment medium is employed (Forest, 1962; MacEntee et al., 1973). Nevertheless, an overall qualitative picture of the importance of algae in soil can be drawn from comparisons of reported numbers of algae in different soils. Table VII, includes a representative sample of numbers of algae in soil.

Diurnal and seasonal fluctuations in numbers have been estimated less often than have single, instantaneous counts. Tchan and Whitehouse (1953) determined, by means of direct microscopic counts of fluorescing algal cells, that there was a dynamic character to the algal community over a 24 hour period. The direct counts were as follows (#s/g): 4750 @ 11 a.m., 2100 @ 2 p.m., 5300 @ 5 p.m., 4500 @ 7 p.m., 1300 @ 8 a.m., and 2500 @ 12 noon. Direct observation of fluorescing cells inside of protozoans and nematodes indicated that predation was a factor, but experimental evidence tended to substantiate their hypothesis that fluctuating moisture was primarily responsible for their observations.

Seasonal fluctuations in floristic diversity have been studied more often than numerical fluctuations. The composition of surface communities of algae on cultivated and uncultivated grassland soils in Oklahoma, Tennessee (Willson, 1957; Willson and Forest 1957), and Washington (Metting, 1979) did not fluctuate during the years in which they were studied. Fluctuations in numbers were estimated by Metting (1979) for cultivated (barley) and uncultivated (native meadow-steppe vegetation) portions of an eastern Washington silt loam. The data summarized in Table VIII, include the highest counts yet reported for temperate soils.

Studies in which soil samples were collected for numerical and/or floristic analysis of the algal community at the same time and in the same manner as samples collected for physical and chemical analysis are few. Yet only this sort of sampling permits a true evaluation of whether community properties are related to microenvironmental properties, either instantaneously or dynamically.

Investigations which were primarily concerned with floristic diversity, but which included analysis of soil properties are those of James (1935; quantified carbonate and determined soil texture), Petersen (1935; texture and pH), Bunt (1954; moisture, temperature, pH, organic C, total N), Singh (1961; moisture, pH, electrical-conductivity, total and available P, total Al, Ca, Fe, Mn), Pandey (1965; moisture, texture, pH, organic C, organic matter), Jurgensen and Davey (1968; moisture and pH); Milliger (1969; texture and pH), Cameron (1969a, 1969b, 1970, 1971, 1972a; moisture, temperature, texture, color, organic C, organic N, pH, electrical-conductivity, cation exchange capacity, phosphate, Ca^{+2} , Cl^- , HCO_3^- , K^+ , Mg^{+2} , Na^+ , NO_3^- , SO_4^{-2} , wind, irradiance, soil humidity and evaporation), Henriksson (1970; moisture and temperature), Nordin and Blinn (1972; pH and electrical-conductivity), Johnson (1974a; moisture, tem-

Table VII
Quantitative estimates of algae in soil (#s/g in surface communities).

Situation	Range or maximum value	Method	Reference
Wheat + farmyard manure (England)	91.00–105,500	Dilution counts	Bristol-Roach, 1927 ^a
Wheat, unmanured (England)	2797–36,599	Dilution counts	Bristol-Roach, 1927 ^a
Pasture (Denmark)	40,000–66,000	Dilution counts	Petersen, 1935 ^a
Garden (Denmark)	200,000	Dilution counts	Petersen, 1935 ^a
Cultivated sandy soil (Denmark)	10,000	Dilution counts	Petersen, 1935 ^a
Botanical garden (Denmark)	200,000–3,000,000	Dilution counts	Petersen, 1935 ^a
Dune (Denmark)	200–2000	Dilution counts	Petersen, 1935 ^a
Heath (Denmark)	20,000	Dilution counts	Petersen, 1935 ^a
Forest (Denmark)	10,000	Dilution counts	Petersen, 1935 ^a
Forest (Germany)	793,000	Dilution counts	Fehér, 1936 ^a
Garden (Australia)	275,000–800,000	Direct counts	Tchan and Whitehouse, 1953 ^a
Semi-arid desert (Australia)	0–440	Direct counts	Tchan and Beadle, 1955
Wheat rhizosphere (Australia)	27×10^3	Dilution counts	Rauatt et al., 1960
Hot and cold deserts, worldwide	0– 10^7 (10^2 – 10^3 commonly)	Dilution counts	Cameron, 1969a, 1971, 1972a
Tobacco (North Carolina)	23,000–165,000	Dilution counts	Schlichting, 1973
Saline tallgrass prairie (North Dakota)	33,819	Enrichment counts	Nordin and Blinn, 1972
Shortgrass prairie (Texas)	30,000–50,000	Dilution counts	Thayer, 1974
Golf course (Texas)	54,159	Plate counts	King and Ward, 1977 ^a
Lawn (Texas)	37,385	Plate counts	King and Ward, 1977 ^a

Table VII
Continued.

Situation	Range or maximum value	Method	Reference
Swale (Texas)	35,069	Plate counts	King and Ward, 1977 ^a
Roadside (Texas)	14,680	Plate counts	King and Ward, 1977 ^a
Woodlot (Texas)	5,736	Plate counts	King and Ward, 1977 ^a
Various soils (New Zealand)	10 ⁴ –10 ⁶	Dilution counts	Cairns et al., 1978
Beech Woods (Italy)	0–8,200	Plate counts	DeSanto et al., 1978
Beech-fir Woods (Italy)	1000–108,000	Plate counts	DeSanto et al., 1978
Cultivated soil (Estonia S.S.K.)	3.1–4.8 × 10 ⁶	Dilution counts	Rahno et al., 1978
1 year-old field (New Jersey)	3.3 × 10 ⁷	Dilution counts	Hunt et al., 1979
11 year-old field (New Jersey)	2.2 × 10 ⁷	Dilution counts	Hunt et al., 1979
Oak-dogwood stand (New Jersey)	1.2 × 10 ⁵	Dilution counts	Hunt et al., 1979
<i>Pinus</i> stand, beneath canopy (Washington)	13,700–137,200	Plate counts	Metting and Rayburn, 1979 ^a
<i>Pinus</i> stand, beyond canopy (Washington)	35,300–124,400	Plate counts	Metting and Rayburn, 1979 ^a
Barley (Washington)	71,000–500,000	Plate counts	Metting, 1979
Meadow-steppe (Washington)	340,000– 110,000,000	Plate counts	Metting, 1979

^a Subterranean populations also counted.

perature, texture, color, organic matter, pH, phosphate, Al⁺³, Ca⁺², Cl⁻, HCO₃⁻, K⁺, Mg⁺², Mn⁺², NH₄⁺, NO₂⁻, NO₃⁻, Henriksson et al. (1975; pH, electrical-conductivity, available P, K, and Mg, NO₃-N, NO₂-N), King and Ward (1977; moisture, pH, total and available P, NO₃-N, NO₂-N), Hunt et al. (1979; moisture, temperature, irradiance, organic C, total N, Mg⁺², Ca⁺², K⁺ and available P), Metting and Rayburn (1979a; moisture, temperature, texture, organic matter, pH, electrical-conductivity, cation exchange capacity, % base saturation, available P, Ca⁺², Mg⁺²,

Table VIII

Plate counts of algae on cultivated and uncultivated portions of a silt loam in eastern Washington state in 1977 (Metting, 1979).

Date		Plat counts (#/g water-free soil)		Soil water (% field cap.)	
		Cultivated portion	Uncultivated portion	Cultiv.	Uncult.
April	3	1.0×10^4	3.4×10^5	22	91
	15	1.4×10^4	3.7×10^5	21	35
	29	1.8×10^4	9.4×10^5	16	15
May	6	1.5×10^4	8.2×10^5	27	35
	20	9.0×10^3	3.4×10^6	75	96
June	10	8.5×10^3	4.4×10^6	27	46
	24	9.7×10^3	7.3×10^6	11	15
July	8	7.1×10^3	1.9×10^6	5	5
	22	1.8×10^4	2.1×10^6	16	20
August	5	7.6×10^3	1.5×10^6	11	10
	19	7.6×10^3	9.8×10^5	5	5
September	2	9.1×10^3	1.3×10^6	53	101
	16	1.5×10^4	5.2×10^5	16	30
October	14	1.6×10^4	2.3×10^6	27	96
	28	2.9×10^4	6.2×10^6	27	112
November	11	3.0×10^4	1.1×10^7	75	96
	27	5.0×10^4	3.4×10^6	176	167

K⁺, Na⁺), and Metting (1979; moisture, temperature, texture, bulk density, organic matter, pH, electrical-conductivity, cation exchange capacity, % base saturation, available P, SO₄-S, Ca⁺², Mg⁺², K⁺, Na⁺, NO₃⁻).

PRIMARY PRODUCTION

The incorporation of organic carbon via photosynthesis, and of organic nitrogen via dinitrogen fixation are the most important contributions that algae make to the fertility of the soil. While providing a constant supply of new carbon and nitrogen, algae also act as a reserve of inorganic nutrients which might otherwise be leached from the root zone. It is for these reasons, in addition to their positive influence on soil structure, that algae are as important in mature soils as they are to community succession.

There is virtually no quantitative data reflecting in situ primary production by soil algae. Gollerbach et al. (1956) estimated that the algae of takyrs soils represented from 0.5 to 1.4 metric tons of organic matter per hectare. No temporal variation was incorporated into their estimate, therefore primary productivity could not be gauged. Fuller and Rogers (1952), in a similar calculation for Arizona soils, estimated that algae were responsible for an annual increment of about 3 English tons of carbon (about 6 tons of organic matter) per million pounds of soil (acre 3" slice). Prasad (1949) determined that the average annual input of algae into six soils was 3750 mg organic carbon per 100 g of soil. *Microcoleus vaginatus*, during warm humid periods, was estimated to represent a maximum of 45 mg organic matter per gram of soil in almond groves at any one time (Markova, 1976).

DINITROGEN FIXATION

The most intensively investigated aspect of soil algology has been asymbiotic dinitrogen fixation by blue-green algae (Fogg, 1956; Watanabe, 1960; Federov and Tellichenko, 1965; Holm-Hansen, 1968; Shtina, 1968; Lie and Mulder, 1971; Jurgensen, 1973; Mishustin et al., 1973; Carr and Whitton, 1973; Fogg et al., 1973; Stewart, 1970, 1971, 1973a, 1973b, 1974, 1977; Dalton, 1974; Quispel, 1974; Pankratova, 1975; Evans and Barber, 1977; Hardy and Gibson, 1977; Mal'tseva, 1977; Peters, 1978; Rychert et al., 1978). Particular attention has been paid to the blue-green algae of rice soils. Information is available from several countries, including INDIA (De and Sulaiman, 1950a, 1950b; Rewari et al., 1961; Singh, 1961; Aiyer, 1965; Venkataraman et al., 1959; Venkataraman, 1966, 1972, 1975), JAPAN (Watanabe et al., 1954; Okuda and Yamaguchi, 1956; Watanabe, 1965; Kobayashi et al., 1967; Watanabe and Yamamoto, 1967, 1971), THE PHILIPPINES (Yoshida et al., 1973; Watanabe et al., 1977), EGYPT (El-Nawawy and Hamadi, 1975), ITALY (Materassi and Balloni, 1965), AUSTRALIA (Bunt, 1961), the SOVIET UNION (Kuchkarova, 1962; Shtina, 1965, 1968, 1969; Pankratova, 1979), SENEGAL (Roger, 1973), IVORY COAST (Raud, 1978), NIGERIA (Moore, 1963), UGANDA (Calder, 1959), KOREA (James et al., 1970), MALAYSIA (Johnson, 1969), and other localities in SOUTHEAST ASIA (Watanabe and Yamamoto, 1971).

Estimates of the number of different edaphic species of blue-green algae which are capable of dinitrogen fixation range from 25 (Singh, 1961) to 38 (Shtina, 1968, 1972), and depend upon the taxonomic system being used. Genera which include species of dinitrogen-fixing algae are: *Anabaena*, *Anabaenopsis*, *Aphanothece*, *Aulosira*, *Calothrix*, *Camptylone-ma*, *Chlorogloea* Wille, *Cylindrospermum*, *Fischerella*, *Fremyella*, *Gloeocapsa*, *Gloeotrichia* Agardh, *Hapalosiphon*, *Lyngbya*, *Mastigocla-*

Scytonema, *Stigonema*, *Tolypothrix*, *Trichodesmium* Ehrenberg, *Westiella*, and *Westiellopsis* (Wyatt and Silvey, 1969; Desikachary, 1973; Stewart, 1973a, 1974; Zimmerman, 1979). While some of these genera have not been shown to include edaphic or hydroterrestrial species, they are included for the purpose of completeness.

Frank (1889) and Beijerinck (1901) were among the first to suggest that blue-green algae could assimilate gaseous nitrogen. Although Pringsheim (1914) and Glade (1914) were able to isolate certain species into pure culture, it was not until 1928 that Drewes unequivocally demonstrated dinitrogen fixation in pure culture with *Anabaena variabilis* and *Nostoc punctiforme* Kützinger. The implications were pointed out by De (1939) and Singh (1940–1941), in reports documenting the fact that successive annual croppings of rice had been produced in the tropics for years without chemical fertilization.

Summarizing 30 years of studies on algal distribution in Japan, south-east Asia, India, and Africa, A. Watanabe reported that dinitrogen-fixing species were widely distributed in both tropical and temperate areas, but were more abundant in the tropics. They comprise about 12% of the total algal flora in the tropics, and about 2% in temperate zones north of 30° latitude (Watanabe and Yamamoto, 1971). The most common tropical species belong to the genera *Anabaena*, *Aulosira*, *Nostoc*, *Scytonema*, and *Tolypothrix* (Singh, 1961). Venkataraman (1975) reported that only 33% of 2213 Indian soil samples contained dinitrogen fixers, and while blue-green algae were widely distributed, certain geographical areas were rich and others relatively poor. For example, 87% of soils from Uttar Pradesh and 60% of soils from West Bengal contained dinitrogen-fixing species, as compared with only 9% and 7% for Kerala and Kashmir. *Nostoc* and *Anabaena* were reported as universal, with species of *Calothrix*, *Cylindrospermum*, *Mastigocladus*, *Westiella*, and *Aulosira fertilissima* Ghose sporadically appearing as dominants (Venkataraman, 1975). Singh (1961) reported *A. fertilissima* to be the most widespread and important blue-green alga associated with rice soils. Other common algae, and their seasonal associations in rice soils are listed in Table IX. Variation due to kinds and application rates of nitrogen fertilizers has been reported (Singh, 1978).

Nostoc commune, *N. sphaericum* Vaucher, *Fischerella muscicola* (Thuret) Gomont, *Tolypothrix tenuis* Kützinger, and *Scytonema* spp. are typical inhabitants of undisturbed soils in the Soviet Union. More moist soils contain *N. paludosum* Kützinger, *Anabaena variabilis*, and *Calothrix elenkinii* Kossinskaja. Special strains of *Anabaena* characterize saline soils, while *N. muscorum* and *N. punctiforme* are ubiquitous (Gollerbach and Shtina, 1969; Shtina, 1969).

Table IX

Dominant blue-green algae and successional trends in rice soils of India (Singh, 1961).

June–July (beginning of wet season):

Aphanothece pallida (Kützinger) Rabenh., *Schizothrix arenaris*, *Porphyrosiphon notarisii* (Meneg) Kütz., *Microcoleus chthonoplastes* (Thuret) Gomont, *Scytonema ocellatum* Lyngbye, *S. hofmanii* Agardh, *Camptylonema lahorensense* Ghose, *Nostoc muscorum* (Ag.) Bornét & Flahault, *N. calcicola* (Breb) Bornét & Flahault, *N. humifusum* (Carm.) Bornét & Flahault, *Cylindrospermum licheniforme* (Kützinger) Bornét & Flahault, *C. gorakhporensense* Singh, *Hapalosiphon welwitschii* West & West, *H. intricatus* W. & G. S. West.

July–August (soil in puddled condition):

Aulosira fertilissima Ghose, *A. cylindrica* Lemm., *Anabaena ambigua* Rao, *A. variabilis* (Kütz.) Bornét & Flahault, *A. oryzae* Fritsch, *Anabaenopsis circularis* (West) Wolosz & Miller, *Cylindrospermum gorakhporensense* Singh, *Fischerella* sp., *Tolypothrix tenuis* Kützinger, *Wollea bharadwajae* Singh.

September–November (climax community of waterlogged soils):

Aulosira fertilissima Ghose, *Anabaena* spp., *Gloeotrichia natans* (Rabenh.) Bornét & Flahault.

After December (post-harvest, soil again exposed):

Aulosira fertilissima Ghose (on drier soils), *Cylindrospermum gorakhporensense* Singh, *C. muscicola* Kützinger, *C. licheniforme* (co-dominant with *A. fertilissima* on moister soils).

In one of the few studies in which a large number of temperate soils were investigated for the presence of dinitrogen-fixing blue-green algae, Granhall (1975) found 66% of 64 Swedish soils to contain blue-green algae, and that 47% contained dinitrogen-fixing strains distributed among seven genera. Shtina (1968), who investigated 15 soils (including two tundra soils) in the Soviet Union, found dinitrogen-fixing algae to be universal, with from one (a virgin, montane soil), to 18 (cultivated, former woodland soil) or 19 (virgin sod-podzolic soil) species per soil. In steppe and desert soils dinitrogen-fixing algae are important components of rain crusts, algal crusts, and lichen crusts (Beadle and Tchan, 1955; Tchan and Beadle, 1955; Shields et al., 1957; Cameron, 1958; Cameron and Fuller, 1960; Fuller et al., 1960; MacGregor and Johnson, 1961; Mayland, 1965; Cameron and Blank, 1966a; Mayland et al., 1966; Mayland and McIntosh, 1966b; Gollerbach and Shtina, 1969; Snyder and Wullstein, 1973; Friedmann and Galun, 1974).

The importance of dinitrogen fixation by free-living blue-green algae, and by lichen phycobionts and moss-algal associations in cold dominated ecosystems is well documented (Holm-Hansen, 1963b, 1964; Cameron et al., 1965b; Gollerbach and Shtina, 1969; Novichkova-Ivanova, 1972a; Alexander and Schell, 1973; Alexander, 1975; Englund, 1978). *Nostoc commune* Vaucher is probably the most widespread dinitrogen fixer, both

as an asymbiont and as the phycobiont in lichens, in both tundra (Tichomirov, 1957; Stutz, 1973; Stutz and Bliss, 1975) and antarctic (Holm-Hansen, 1964; Fogg and Stewart, 1968; Cameron, 1970) soils.

The abundance, or standing crop of dinitrogen-fixing algae in soils has been estimated by determining nitrogen content (total, organic-N, $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$), or by direct and dilution counts of cells, filaments, or plant masses. Due to variation in counting methods, direct comparisons of numbers presented by different scientists does not necessarily represent a true comparison of the relative importance of the algae. Estimates of the abundance of dinitrogen-fixing algae range from zero (in some polar, temperate, and tropical soils) to 18 million filaments of *Cylindrospermum licheniforme* per gram of soil in India (Singh, 1961). Shtina (1968) reported 3.5–4.1 g of *Nostoc commune* per m^2 on a rendzina soil, 200,000 *N. commune* cells per cm^2 on chestnut, and 575,000 on dark-chestnut soils. Up to 150 *N. sphaeroides* colonies per cm^2 on alluvial soil and up to 310,000 *C. licheniforme* cells per cm^2 on sod-podzolic soils were also reported. While solonetz soils support up to 12 million cells per cm^2 (Shtina and Bolyshev, 1960), numbers do not usually exceed 1000 to 5000 cells per g of soil in temperate soils in the Soviet Union (Shtina, 1972).

Jurgensen and Davey (1968) reported numbers of blue-green algae per g of soil for surface and subterranean samples from an acid forest nursery, from Alaskan tundra, and from a number of woodland habitats in North Carolina. All of the samples from the nursery soil, on two different dates, contained blue-green algae. Numbers ranged from 48,000 per g to 96,000 per g on the surface, and from 1600 per g to 13,300 per g for the 5–10 mm level. Dinitrogen-fixing algae were not found in any of the nine Appalachian mountain soils sampled, or in two of five soils from the Piedmont, or in five of seven from the Atlantic Coastal Plain. Woodland soils with blue-green algae included two sites dominated by loblolly pine (with 130 and 640 algae/g), one site supporting a shortleaf pine-red oak-hickory stand (1200 algae/g), one stream bottom site supporting beech (160 algae/g), and one soil dominated by cypress (16,500 algae/g). Sites in Alaska were reported to support from zero dinitrogen-fixing algae per g in birch-heather and level grass dominated communities, to 6200 per g on a soil of a willow-moss community. Although the Alaskan soils with dinitrogen-fixers ranged in pH from 5.8 to 6.5, it was reported that the soils from North Carolina (including the nursery) all had a pH of less than 6.0. The sample from which the 96,000 per g count originated had a pH of 5.8 and 13.2% moisture by weight (Jurgensen and Davey, 1968). The most probable number of blue-green algal particles per g of soil in eastern Washington fluctuated from 0–180 per g, and from 67.0–160,000 per g in cultivated and uncultivated silt loams (respectively) (Metting, 1979; Zimmerman et al., 1980).

Data which have been collected in attempts to quantify the importance of blue-green algae to the nitrogen status of the soil can also be used as a measure of the standing crop. Shields et al. (1957), evaluated several surface crusts of arid lands in New Mexico for their Kjeldahl (total) N, $\text{NO}_2\text{-N} + \text{NO}_3\text{-N}$, and amino-N contents on three different dates. Amino nitrogen averaged 256 mg/kg of alga-stabilized gypsum crust compared to 10 mg/kg of soil six inches below the surface in June. Total $\text{NO}_3 + \text{NO}_2\text{-N}$ in June averaged 5.6 mg/kg of crust, and 0.45 mg/kg of soil at six inches. Differences among dates were insignificant. Algal crusts on lava soils averaged 1031 mg total N/kg, a value less than for lichen-stabilized crusts (1553 mg/kg), but far greater than bare soil (225 mg/kg of soil).

Algae are responsible for a difference in total nitrogen of from 77–133% in rice soils as compared with soils without algae (Marathe and Anantani, 1975). Under fescue grass in the southeastern United States, blue-green algal crusts include 2.76% total C and 0.18% total N compared with 0.67% and 0.06% on fallow soil without a crust (Reddy and Giddens, 1975). The data of Prasad (1949) are summarized in Table X. Numbers are the average values for six soils, and represent the nitrogen content of four square feet of dried blue-green algal incrustation, sampled during the dry season, as compared with the soil beneath the algae.

A better estimation of the nitrogen contribution to soils by blue-green algae can be made based on estimates of rates of dinitrogen fixation in laboratory and greenhouse (pot) cultures, and in the field. Table XI includes data collected from rice paddies and pot cultures, as well as estimates of dinitrogen fixation in temperate soils. Gains of less than 100 kg/ha/yr are difficult to assess for two reasons. First, it is hard to construct sampling procedures which accurately reflect natural conditions and are comparable among investigators. Second, the acetylene reduction method (Hardy et al., 1973), which is the easiest and most popular technique, is based on the assumption that there is a fixed ratio of acetylene reduced to dinitrogen fixed, an assumption shown by ^{15}N studies to be invalid for field work due to great variability among soils (Hardy et al., 1973).

Values for temperate and tropical soils are alike, with tropical rates ranging up to 69 kg dinitrogen fixed per ha during a six week period in pot culture with rice (De and Mandal, 1956). Yoshida et al. (1973), estimated that up to 870 kg were fixed per ha per year in Philippine soils, based on pot culture experiments. Temperate soils with blue-green algae may fix up to 51 (Henriksson, 1971) or 94 (Granhall and Selander, 1973; Granhall, 1975) kg of dinitrogen per ha per yr. However, diurnal and seasonal fluctuations in activity of dinitrogen-fixing blue-green algal populations are not well documented, and most estimates are based on quantifications made during the growing season. Maximal rates for temperate

Table X

Average nitrogen and carbon content of algae and soil beneath the algae for six rice soils in India (after Prasad, 1949).

	mg/100 g of algae	mg/100 g soil
Weight of 4 ft ² of algae	148.30	NI
NH ₄ -N	40.27	0.7
NO ₃ -N	0.85	0.8
organic N	329.74	36.0
total N	370.74	29.9
organic C	3753.	NI
total C	NI	377.
C/N	10.1	12.9

NI = no information.

soils with blue-green algae during summer months, include 40 $\mu\text{g N}_2$ fixed/m²/h in arable Scottish soils, 140 $\mu\text{g N}_2$ /m²/h in Scottish pasture (Fogg et al., 1973), and 0.06 to 25.7 mg/m²/h (Granhall, 1975) to 11 mg/m²/day (Granhall and Selander, 1973) in tilled and virgin Swedish soils and 6–10 g N/ha/hr in soils of England and Wales (Lockyer and Cowling, 1977).

The best evidence for the importance of asymbiotic dinitrogen fixation in temperate soils has been provided by the Broadbalk experiment at the Rothamsted Experimental Station in England. The upper 20 cm of soil in stubbed (woody plants continuously cut back) and wooded plots has been monitored for total N since 1882. Due in part to algal fixation, and in part to bacterial fixation in dicot rhizospheres, the soils have accumulated about 2000 kg N per ha, an average annual increment of 39 kg for the stubbed plot and 49 kg for the wooded plot (Dart and Day, 1975; Witty and Dart, 1977).

Reviewing the literature on dinitrogen fixation by free-living blue-green algae in cold dominated ecosystems, Alexander (1975) listed estimated values for nitrogen input into soils. Estimates based on in vitro acetylene reduction assays varied greatly, ranging from 0.002 mg N/m²/yr for tundra soils of Devon Island, Canada, dominated by *Nostoc commune* (Stutz, 1973), to 11,500 mg N/m²/yr for a mire in Sweden dominated by various vascular species (Granhall and Selander, 1973). Estimates for soils of diverse habitats (heath, meadow, birchwood stands, snow) in Norway ranged from 100–250 mg N/m²/yr (Torsvik, 1971). Horne (1972) reported rates of up to 2.4 mg N/m²/yr from Antarctica.

In a comparison of dinitrogen fixation between six Swedish and six Indian soils, Henriksson et al. (1975) reported that the temperate soils had a greater capacity (2.1 g N fixed/g soil/h) than the tropical soils (0.45

Table XI

Estimates of annual or seasonal rates of dinitrogen fixation in soils with populations of blue-green algae.

Situation	kg/ha	Reference
Rice paddy (India)	70/yr	Willis and Green, 1948
Pot culture of soil from rice soil + P amendment (India)	18–69/6 weeks	De and Mandal, 1956
Pot culture of soil from rice soil, minus P amendment (India)	15–49/6 weeks	De and Mandal, 1956
Maize field (India)	80/yr	Singh, 1961
<i>Tolypothrix tenuis</i> crusts (Japan)	22/yr	Watanabe et al., 1951
Pot culture, soil + rice + algae (Philippines)	10–55/yr	MacRae and Castro, 1967
Pot culture, soil + rice + algae (Philippines)	40–80/yr	Yoshida et al., 1973
Cornfield (Germany)	2/yr	Jahnke, 1967
<i>Artemisia</i> steppe (Arizona)	10.9/yr	Mayland and McIntosh, 1966b
Wheatfield with <i>Nostoc</i> (Sweden)	15–51/yr	Henriksson, 1971
Lakeside meadow with <i>Nostoc</i> , <i>Anabaena</i> , <i>Calothrix</i> , and <i>Cylindrospermum</i> (Sweden)	4–44/yr	Henricksson, 1971
Slack dune (England)	25/yr	Stewart, 1967b
Various soils (Sweden)	up to 94/yr	Granhall and Selander, 1973
Algal crusts Great Basin (United States)	10–100/yr	Rychert and Skujins, 1974
Oldfield, wooded (England)	49/yr	Dart and Day, 1975
Oldfield, stubbed (England)	39/yr	Dart and Day 1975
Wheat (England)	48/yr	Dart and Day, 1975

g N fixed/g soil/h), in the laboratory. Maximum fixation rates for the soils were recorded at 20°C for Swedish samples and at 25°C for the Indian samples. Differences were not related to pH or nutrient content, although the sample with the least activity had the greatest ionic strength as estimated by electrical-conductivity.

Whether cultivated or uncultivated, temperate soils support more active populations of dinitrogen-fixing algae has not been firmly established. Henriksson et al. (1972a) found values for virgin soils to be similar to wheatfields (see Table XI). Others (Jahnke, 1967; Paul et al., 1971; Vlasak et al., 1973) contend that dinitrogen fixation by asymbionts is not significant in either tilled or virgin grassland soils in North America. Woodmansee (1978) agreed, adding only that the blue-green algae may

yet be shown to be important in steppe zones, in either cultivated or uncultivated soils. Numbers of heterocystous algae are reduced by farming practices in eastern Washington (Zimmerman, 1979; Zimmerman et al., 1980), while in contrast, temperate soils in the Soviet Union tend to increase in numbers of dinitrogen-fixing algae upon cultivation. For example, the ratio of nostocacean to oscillatoriacean algae in sod-podzolic soils increased, upon cultivation, from 1:3 or 1:2, to 2:3 or 5:1 (Shtina, 1972).

Fogg (1947, 1949, 1956) and others (Allen, 1956a; Bunt, 1961; Venkataraman, 1961b; Varma et al., 1964; Gollerbakh and Shtina, 1969; Shtina, 1972; Fogg et al., 1973; Ohmori and Hattori, 1974; Reddy and Giddens, 1975; Lockyer and Cowling, 1977) have suggested that limited fixation by blue-green algae in cultivated soils and laboratory culture is due to the introduction of combined sources of nitrogen via fertilization and irrigation. For example, aliphatic amines up to 6 C long inhibited O_2 production and dinitrogen fixation by *Anabaena subcylindrica* as much as 2500 times more than did NH_3 (Mosier, 1978). However, evidence for the hypothesis that this might be a non-specific salt effect has come from soil (Henriksson et al., 1975) and laboratory (Kennedy, 1970; Stewart et al., 1975) data. On the other hand, Bortels (1940), De and Mandal (1956), and Shtina (1969) showed that an increase in growth of potential dinitrogen-fixing algae accompanied application of nitrogen alone, or in combination with K or P. It may be that these contradictory interpretations are due to factors within the surface few mm of the soil, in which the active populations of algae reside, with variations in physical or chemical properties being responsible for differential leaching of nutrients away from the algae (Henriksson et al., 1975).

Light is required by diazotrophic soil algae as the ultimate source of energy and reducing power for dinitrogen fixation (Granhall, 1970; Rinaudo et al., 1971; Stanier, 1974; Balandreau et al., 1974). Although *Nostoc muscorum* and *Anabaenopsis circularis* (Watanabe and Yamamoto, 1967), and other species (Allison et al., 1937; Fay, 1976; Jones, 1977a) can fix dinitrogen in the dark with glucose as an energy source, nitrogenase activity has never been detected from below the surface of a soil on which algae are active fixers (Henriksson et al., 1972b). In situ acetylene reduction assays have demonstrated that nocturnal fixation in rice soils (Alimagno and Yoshida, 1977) and in subtropical stands of *Pennisetum* Rich. (Jones, 1977b) follows active photosynthesis during the day. Fluctuations in dinitrogen fixation rates by soil algae in Morocco coincided with diurnal changes in isolation, and may have been inhibited at mid-day by irradiances of 40–50,000 lux (Renaut et al., 1975), while some strains isolated from northern Sweden do not have nitrogenase activities saturated by light (Granhall, 1975). Dinitrogen fixation by mats of blue-

green algae in *Pennisetum* swards is also inhibited by high irradiance (Jones, 1977b). An Egyptian strain of *Nostoc commune*, grown in laboratory culture, showed optimum growth and fixation at 6000 lux (Taha and El-Refai, 1963a). Fixation by algal crusts in the American Great Basin steppe is optimal at 200 microeinsteins $\text{cm}^{-2} \text{second}^{-1}$ (Rychert & Skujins, 1974).

Temperature is important, as indicated by comparative studies of dinitrogen fixation in Swedish and Indian soils, as mentioned above (Henriksson et al., 1975). Samples collected from Scottish soils in the winter, fixed dinitrogen in the laboratory at 15°C, but not at 4°C (Fogg et al., 1973). Whereas *Westiellopsis prolifica* Janet showed greatest growth at 40°C in laboratory studies, dinitrogen fixation rates were maximal between 30 and 35°C (Pattnaik, 1966). Both pre-dawn low temperatures and mid-day highs suppressed in situ fixation by blue-greens associated with *Pennisetum* (Jones, 1977c). Adaptation to low temperatures by algae of high latitudes and altitudes is responsible for fixation of significant amounts of dinitrogen in many instances (Holm-Hansen, 1963b; Fogg and Stewart, 1968; Horne, 1972; Kallio and Kallio, 1975).

In general, greater growth of dinitrogen-fixing blue-green algae is found on moister soils in both tropical (Singh, 1961; Venkataraman, 1975) and temperate zones (Granhall and Henriksson, 1969; Shtina, 1972). The importance of moisture was demonstrated with dried Broadbalk (England) soils, which when rewetted in the laboratory, showed nitrogenase activity within two hours (Witty, 1974). Activity of *Nostoc muscorum* crusts following desiccation is proportional to the degree to which they are rewetted (Rodgers, 1977). Optimum soil moisture varies with the species of alga. Growth of *Scytonema ocellatum* in lawns and grasslands in India is greatest at 40% of the soil's water holding capacity (Singh, 1942), and while optimal fixation in *Pennisetum* swards is between 22 and 42% (Jones, 1977d), most species show optimum dinitrogen fixation at between 80 and 100% (Singh, 1961; Tret'yakova, 1965; Shtina, 1972; Rychert and Skujins, 1974).

Low soil pH has often been cited as an important factor limiting the distribution and dinitrogen-fixing activities of blue-green algae (Brannon, 1945; Lund, 1962; Shields and Durrell, 1964; Gollerbach and Shtina, 1969; Fogg et al., 1973; Zimmerman, 1979). Blue-green algae were found to be less abundant on acidic soils in Sweden, Germany, and Andorra, than on neutral to alkaline soils (Granhall and Henriksson, 1969; Henriksson et al., 1972b). In general, optimal levels of pH for growth and dinitrogen fixation are neutral to alkaline (Fogg et al., 1973). For example, optimal pH ranges for some algae are: 7.0–8.5 for *Nostoc muscorum* (Allison et al., 1937), 6.6–10.0 for *Aphanothece* sp. (Singh, 1974a), 7.4–9.0 for species of *Anabaena* (Granhall, 1970; Smith and Evans, 1970; Haystead

and Stewart, 1972), and 7.0 for *Gloeocapsa* sp. (Gallon et al., 1972). However, reports by Jurgensen and Davey (1968) for Alaska and North Carolina, James et al. (1970), who found dinitrogen fixers in acidic soils in Korea, and Dooley and Houghton (1974), who demonstrated nitrogenase activity by three species of *Anabaena* isolated from peat soils, all suggest that pH alone is not always limiting. For example, the pH optimum for *Nostoc punctiforme* was found to be 7.6, but nitrogenase activity was detected in culture from pH 5 to 10.5 (Granhall, 1970).

Other factors which influence blue-green algal nitrogenase activity are ionic strength and oxidation-reduction potential. That high salt concentrations might limit fixation has been mentioned. Biochemical studies show that high levels of O_2 inhibit fixation, especially by non-heterocystous blue-greens (Stewart and Pearson, 1970; Stewart, 1971, 1975). Data from studies of waterlogged rice soils suggest that reducing conditions favor dinitrogen fixation (Singh, 1961).

Since it is known that ATP is required for algal nitrogenase activity (Stewart, 1975), the repeated observation that increased phosphorus in soil and freshwater systems stimulates fixation might be attributed to increased ATP synthesis (Dhar and Bhat, 1965; Stewart and Alexander, 1971; Stewart et al., 1975). Stimulation has been noted for algae in pot cultures with rice (De and Mandal, 1956), in field experiments with $CaCO_3 + K_2HPO_4$ (De and Sulaiman, 1950a; Okuda and Yamaguchi, 1955; Varma et al., 1964) in lake waters with inorganic and detergent phosphates (Stewart and Alexander, 1971), and in soils with insoluble $CaPO_4$ (De and Sulaiman, 1950a). Stewart (1971) stated that inorganic P promotes better growth of cyanophytes than do organic sources.

It has been shown that algal nitrogenase activity in pure culture is dependent upon a supply of Mo, Ca, and Na, and that Co is required for growth (Allen and Arnon, 1955a; Holm-Hansen et al., 1954; Allen, 1956a; Eyster, 1958; Taha and El-Refai, 1962b; Okuda et al., 1962). Molybdenum is not required for NO_3^- assimilation by *Anabaena cylindrica* or *Cylindrospermum sphaericum* (Wolfe, 1954; Venkataraman, 1958), although its presence promotes healthier growth. Maximal growth of *A. cylindrica* with NO_3^- as the nitrogen source occurs at 0.075 to 0.100 ppm Mo, a value equal to about one-third of the optimal requirement with N_2 as the sole source (Wolfe, 1954). Jacobs and Lind (1977) found the optimal concentration of Mo to vary with temperature, being greatest (50 $\mu g/l$) at 30°C and less at 15°C (15 $\mu g/l$) and 23°C (5 $\mu g/l$). Molybdenum concentration does not affect growth with NH_4Cl (Wolfe, 1954). Sodium is required in amounts greater than 5 ppm for optimal fixation in the absence of combined nitrogen (Allen and Arnon, 1955a; Eyster, 1972). Vanadium cannot replace Mo as it can to some extent in *Azotobacter*, nor can Sr replace Ca (Allen and Arnon, 1955b; Taha and El-Refai, 1962b). Calcium content

of soils may be important for improvement of the quality of the ionic environment by alleviating the deleterious effects of high concentrations of salts through precipitation of excess anions.

Evidence from field work includes the positive effect on algal development in rice soils of fertilization with CaCO_3 (Okuda and Yamaguchi, 1955). In laboratory culture, dinitrogen fixation by *Aulosira fertilissima* was stimulated by addition of CaCO_3 , KH_2PO_4 , MgSO_4 , or $\text{CaCO}_3 + \text{KH}_2\text{PO}_4$, but was depressed when all three were simultaneously incorporated into the medium (Varma et al., 1964). Liming of soil under fescuegrass increased dinitrogen fixation in the southeastern United States (Reddy and Giddens, 1975). Also, Henriksson et al. (1972b) found that laboratory nitrogenase activity in soil cores from three European countries decreased in the following order: high Ca soils, loessal soils, limestone soils, mull = 0. Calcium-rich soils in the Soviet Union also tend to support more diverse and active populations of dinitrogen-fixing blue-green algae (Balezina, 1965; Shtina, 1972). The effects on dinitrogen fixation by blue-green algae of clay mineralogy and soil pollution with heavy metals, are unknown, although blue-green algae in rice soils have been shown to accumulate Cd up to 10,000 times its concentration in the water (Reiniger, 1977).

SOIL ALGAE AND AGRICULTURE

GENERAL CONSIDERATIONS

The most important consequences of algal growth in soil to agriculture are the input of carbon and nitrogen, and the positive effects on soil structure and erosion control. To date, algal populations in cultivated soils have been manipulated for three different, yet interrelated purposes. These include inoculation of paddy soils with dinitrogen-fixing species for the purpose of supplying combined nitrogen, the use of aquatic and edaphic algal growth as green manure, and the inoculation of unproductive soils with green or blue-green algae in order to effect reclamation of the soil through improved structure. The effects of algae on crops is due also, in unknown measure, to their production of hormone and vitamin-like compounds which may stimulate root growth or beneficial activity by other microorganisms (Venkataraman and Neelakantan, 1967; Venkataraman, 1972).

NITROGEN INPUT

The results of inoculation of rice soils with dinitrogen-fixing species of blue-green algae have been summarized (Subrahmanyam, 1972; Venkataraman, 1972). Increased yields of between 5 and 30% have been reported from China (Ley, 1959; Ley et al., 1959a, 1959b), Vietnam (Mi-

Table XII

Yield of rice straw and grain (kg/ha) in fields with and without a blue-green algal inoculum, as compared with fertilizer treatments (Subrahmanyam et al., 1965b).

Treatment	Grain yield		Straw yield	
	+ algae	- algae	+ algae	- algae
Untreated	1797	2195	1994	2275
(NH ₄) ₂ SO ₄	2463	NI	2630	NI
Lime + superphosphate + Na-molybdate	3001	3979	3145	4327

NI = no information.

shustin, 1964), the Philippines (Watanabe et al., 1977); Japan (Watanabe 1959a, 1962; Huang, 1978); Egypt (Nawawy et al., 1958), the Soviet Union (Perminova, 1964; Shtina, 1965), and India. In India, Subrahmanyam and co-workers (Relwani and Subrahmanyam, 1963; Subrahmanyam and Sahay, 1964, 1965; Subrahmanyam et al., 1964a, 1964b, 1965a, 1965b) tested the influence of different algal mixtures on yields of grain and straw in field tests over a five year period. No differences among varieties of rice were noted. Applied at rates equivalent to 200 g (wet wt.) per ha were *Anabaena* + *Nostoc* + *Phormidium* + *Aphanothece*, or *Anabaena* + *Nostoc* + *Scytonema* + *Tolypothrix*. Results were compared with uninoculated fields, fields fertilized with lime + superphosphate + Na-molybdate, fields fertilized with (NH₄)₂SO₄, and fields fertilized with the first three chemicals and inoculated with algae. Also assessed were the effects of rabbing (burning) as a measure of control of wild populations of algae. They found that rabbing altered the floristic makeup and dominance patterns within the algal communities without affecting rice yields. *Anabaena* dominated all plots except the uninoculated control, which was dominated by *Cylindrospermum* sp., and the burned, and burned and fertilized plots which were dominated by species of *Rivularia* and *Gloeotrichia*. Similar results were obtained by Jagnow (1973) from experiments in which K₂HPO₄ and Na₂MoO₄ were employed.

In Table XII are summarized the effects on yield of grain and straw of the *Anabaena* + *Nostoc* + *Scytonema* inoculum. It can be seen that inoculation with dinitrogen-fixing blue-green algae increased yields by up to 30%, depending upon fertilizer amendments. The positive effect was found to be residual, with algal growth acting as a green manure and sustaining improved yields for two or three years without additional treatment. Other positive effects included reduced competition from vascular and algal "weeds" (viz. *Euglena* and *Spirogyra*).

In an earlier study, Relwani and Manna (1964) found that grain and straw yields in plots fertilized with *Nostoc* + *Tolypothrix* sp., and *Wes-*

Table XIII
Effects of herbicides on algae in soil.

Herbicide	Reference
NEGATIVE EFFECTS	
2,4-D (high rates)	Platonova, 1967a, 1967b
2,4-D	Cullimore and McCann, 1977
amizole	Kiss, 1966
atrazine	Kiss, 1966; Atkins and Tchan, 1967; Pantera, 1970; Hauke-Pacewiczowa, 1971; Mikhailova and Kruglov, 1973
Chlorpropham	Hauke-Pacewiczowa, 1971
dinoseb	Hauke-Pacewiczowa, 1971; Lewis et al., 1978
diuron	Kiss, 1966
EPTC (temporary)	Mikhailova and Kruglov, 1973
granoxone (1st 24 hours)	Anderson and Drew, 1976
lannate (N ₂ fixation)	Huang, 1978
linuron	Pantera, 1970; Sivasithamparam, 1970; Hauke-Pacewiczowa, 1971
MCPA	Hauke-Pacewiczowa, 1971; Cullimore and McCann, 1977
methabenzthiazuron	Huge, 1970
metham sodium (non-sandy soils)	Hauke-Pacewiczowa, 1971
monolinuron	Beck, 1969
monuron	Kiss, 1966; Pantera, 1970
paraquat (1st 24 hours)	Anderson and Drew, 1976
PCP	Ishizawa and Matsuguchi, 1966
propanil	Sharabi, 1969
sevin (N ₂ fixation)	Huang, 1978
simazine	Kaiser and Reber, 1970; Balezina, 1967
TCA	Balezina, 1967; Pantera, 1970
trifluralin	Cullimore and McCann, 1977
venzan	Malkomes, 1977b
verindal FF	Borowiec et al., 1975
POSITIVE EFFECTS	
DNOC	Balezina, 1967
EPTC (long-term effect)	Mikhailova and Kruglov, 1973
MCPA (pot experiments with high H ₂ O content)	Balezina, 1967
prometryne (long-term effect)	Pantera, 1970
simazine (long-term effect)	Pantera, 1970
TCA (pot experiments with high H ₂ O content)	Balezina, 1967

Table XIII
Continued.

Herbicide	Reference
NEUTRAL EFFECTS	
2,4-D (low rates)	Platonova, 1967a, 1967b
2,4-D	Calle, 1970
2,4-D (rice paddy algae)	Venkataraman and Rajyalakshimi, 1972
2,4-D + picloram	Arvik et al., 1971
2,4,5-T	Calle, 1970
gramoxone (after 24 hours)	Anderson and Drew, 1976
linuron	Lewis et al., 1978
metham sodium (sandy soil)	Hauke-Pacewiczowa, 1971
metribuzin	Arvik et al., 1973; Lewis et al., 1978
paraquat (after 24 hours)	Anderson and Drew, 1976
picloram + 2, 4-D	Arvik et al., 1971
prometryne	Platonova, 1967b
propazine	Kaiser and Reber, 1970
siduron	Fields and Hemphill, 1968
simazine	Platonova, 1967b
TCA	Balezina, 1967
trifluralin	Lewis et al., 1978

tiella sp. + lime + superphosphate + Na-molybdate, were greater than for plots fertilized with urea + lime + superphosphate + Na-molybdate. Similar reports of improved yields of rice in India due to algalization include those of Jha et al. (1965), in which a 36% increase was attributed to *Tolypothrix tenuis*, and of Singh (1961), who reported a 114.8% increase in yield upon inoculation with *Aulosira fertilissima*.

In Japan, large scale trials at 11 experimental stations over a five year period showed that inoculation with *Tolypothrix tenuis* resulted in positive annual increments in the yield of rice of 2.7%, 8.4%, 19.1% and 21.8%, on the average (Watanabe, 1959a, 1962). Technical problems and solutions associated with mass culture, distribution, and inoculation have been addressed (Watanabe 1959b, 1959c; Watanabe et al., 1959; Venkataraman, 1961b, 1966, 1972).

In temperate zones, inoculation of soils with algae has not often been attempted. Field experiments at Rothamsted (England), in which inoculation of wheat plots with *Nostoc punctiforme* and *N. ellipso sporum* were attempted, showed that while inoculation accounted for earlier algal growth relative to control plots, there were no significant differences in yield (Froggatt et al., 1972). Neither has algalization of wheat fields in

Table XIV
Effects of herbicides on algae in culture.

Herbicide	Reference
NEGATIVE EFFECTS	
2,4-D (N ₂ fixation)	Inger, 1970; Lundquist, 1970
2,4-D (<i>Chlorella pyrenoidosa</i>)	Bertagnolli and Nadakavukaren, 1970
amitrole (N ₂ fixation)	DaSilva et al., 1975
amitrole (<i>Chlorella</i> spp.)	Vance and Smith, 1969; Wolf, 1962; Adachi and Hamada, 1971; Helling et al., 1971
amitrole (green algae)	Atkins, 1965; Torres and O'Flahery, 1976
atrazine (<i>Chlorella vulgaris</i> , reversible by glucose)	Ashton et al., 1966
atrazine (<i>C. pyrenoidosa</i>)	Zweig et al., 1963; Loeppky and Tweedy, 1969
atrazine (<i>Chlamydomonas reinhardtii</i> autotrophic growth)	Loeppky and Tweedy, 1969
barban (various algae)	Wright, 1972, 1978
barban (<i>C. pyrenoidosa</i>)	Wright, 1972, 1975a, 1975b
bromacil (<i>Chlorella ellipsoidea</i>)	Sumida and Ueda, 1973
captafol (green algae)	Bisiach, 1972
chlorothaldimethyl (various algae)	Fields et al., 1967; Hemphill and Fields, 1967
chlorpropham (<i>Chlorella</i> spp.)	St. John, 1971; Wright, 1972, 1975a, 1975b; Virmani, 1973
coratron (blue-green algae)	Venkataraman and Rajyalkshimi, 1972
coratron (<i>Chlorella</i> sp.)	Sikka and Pramer, 1967
coratron (<i>E. gracilis</i>)	Sikka and Pramer, 1967
dacthal W-75 (<i>Chlorella</i> sp. and <i>Scenedesmus</i> sp.)	Vance and Smith, 1969
dalapon (blue-green algae)	Venkataraman and Rajyalkshimi, 1972
diallate (various algae)	Metting and Rayburn, 1979b
dicryl (blue-green algae)	Shilo, 1965
dicryl (green algae)	Zweig et al., 1963
dinitramine (<i>C. vulgaris</i>)	Belles, 1972
dinoseb (<i>Chlorella</i> spp.)	Kratky and Warren, 1971; Thomas et al., 1973
diquat (various algae)	Zsuzanna and Mihaly, 1977
diquat (blue-green algae)	DaSilva et al., 1975
diquat (<i>Chlorella</i> spp.)	Shilo, 1965; Zweig et al., 1968; Tsay et al., 1970; Adachi and Hamada, 1971; Helling et al., 1971; Thomas et al., 1973

Table XIV
Continued.

Herbicide	Reference
dithane (blue-green algae)	Venkataraman and Rajyalkshimi, 1972
diuron (N ₂ fixation)	Venkataraman and Rajyalkshimi, 1972
diuron (blue-green algae)	Shilo, 1965; Venkataraman and Rajyalkshimi, 1972; Virmani, 1973
diuron (<i>C. ellipsoidea</i>)	Adachi and Hamada, 1971; Sumida and Ueda, 1973
diuron (<i>C. vulgaris</i>)	Geoghegan, 1957
diuron (high rates, <i>Chlorella</i> sp. & <i>Chlamydomonas</i> sp.)	Pillay and Tchan, 1970, 1972
fenuron (<i>C. pyrenoidosa</i>)	Wright, 1972, 1975a
fenuron (<i>C. vulgaris</i>)	Geoghegan, 1957
fenuron (<i>Chlorella</i> sp.)	Sikka and Pramer, 1968
fluometuron (<i>C. pyrenoidosa</i>)	Blythe and Frans, 1972
fluometuron (<i>Chlorella</i> sp., <i>Euglena</i> sp., autotrophic growth)	Sikka and Pramer, 1968
folpet (green algae)	Bisiach, 1972
gramoxone W (various algae)	Anderson and Drew, 1976
linuron (various blue-green algae)	Venkataraman and Rajyalkshimi, 1972
linuron (<i>Chlorella</i> spp.)	Helling et al., 1971; Kratky and Warren, 1971; Thomas et al., 1973
machete (<i>Nostoc muscorum</i>)	Singh and Vaishampayan, 1978
MCPA (N ₂ fixation)	Inger, 1970; Lundquist, 1970; DaSilva et al., 1975
MCPA (various algae)	Sheenan and Fletcher, 1965; Kirkwood and Fletcher, 1970; Metting and Rayburn, 1979b
MCPB (various algae)	Sheenan and Fletcher, 1965; Kirkwood and Fletcher, 1970
methbenzthiazuron (various algae)	Huge, 1970
metobromuron (<i>C. pyrenoidosa</i> , <i>Chlamydomonas</i> sp.)	Loeppky and Tweedy, 1969
metribuzin (various algae)	Arvik et al., 1973
monuron (various algae)	Palmer and Maloney, 1955; Mikhailova and Kruglov, 1973
monuron (<i>C. pyrenoidosa</i>)	Wright, 1972; 1975a
monuron (<i>C. vulgaris</i>)	Geoghegan, 1957
monuron (<i>Chlorella</i> sp.)	Maloney, 1958; Addison and Bardsley, 1968; Cho et al., 1972

Table XIV
Continued.

Herbicide	Reference
monuron (<i>Chlorella</i> sp. and <i>Chlamydomonas</i> sp.)	Pillay and Tchan, 1970; 1972
neburon (<i>Chlorella</i> sp. and <i>Chlamydomonas</i> sp.)	Pillay and Tchan, 1970; 1972
paraquat (various algae)	Anderson and Drew, 1976
paraquat (blue-green algae)	Brooker and Edwards, 1973; DaSilva et al., 1975
paraquat (<i>Chlorella</i> spp.)	Shilo, 1965; Tsay et al., 1970; Adachi and Hamada, 1971; Kratky and Warren, 1971; Thomas et al., 1973
picloram (various algae)	Arvik et al., 1971
prometryne (<i>Chlorella</i> spp.)	Addison and Bardsley, 1968; Helling et al., 1971; Kratky and Warren, 1971; Thomas et al., 1973
propachlor (<i>Chlorella</i> spp.)	Addison and Bardsley, 1968; Helling et al., 1971; Kratky and Warren, 1971; Thomas et al., 1973
propanil (blue-green algae, high rates)	Ibrahim, 1972
propanil (<i>Anabaena cylindrica</i>)	Wright et al., 1977
propanil (<i>Chlorococcum aplanosporum</i>)	Sharabi, 1969
propazine (various blue-green algae)	Venkataraman and Rajyalkshimi, 1972
propham (blue-green algae)	Wright, 1972, 1978
propham (<i>C. pyrenoidosa</i>)	Wright, 1972, 1975a, 1975b
semetryne (<i>Chlorella</i> sp.)	Adachi and Hamada, 1971
siduron (<i>C. vulgaris</i>)	Fields and Hemphill, 1968
simazine (various algae)	Atkins, 1965; Torres and O'Flaherty, 1976
simazine (<i>Dictyococcus</i> sp.)	Flueckiger, 1976
swep (<i>C. ellipsoidea</i>)	Sumida and Ueda, 1973
trichloracetate (<i>C. vulgaris</i>)	Hassall, 1961

POSITIVE EFFECTS

	Sumida and Ueda, 1973
benthiocarb (<i>C. ellipsoidea</i>)	Sumida and Ueda, 1973
DBN (<i>C. ellipsoidea</i>)	Metting and Rayburn, 1979b

Table XIV
Continued.

Herbicide	Reference
diallate (low rates, <i>Nostoc</i> sp.)	Loeppky and Tweedy, 1969; Thomas et al., 1973
diphenamid (green algae)	Sumida and Ueda, 1973
diquat (<i>C. ellipsoidea</i>)	Pillay and Tchan, 1970, 1972
diuron (low rates, <i>Chlorella</i> sp. and <i>Chlamydomonas</i> sp.)	Sumida and Ueda, 1973
EPTC (<i>C. ellipsoidea</i>)	Sumida and Ueda, 1973
HE-314 (<i>C. ellipsoidea</i>)	DaSilva et al., 1975
linuron (N_2 fixation, following temporary inhibition)	Metting and Rayburn, 1979b
MCPA (low rates, <i>Nostoc</i> sp.)	Loeppky and Tweedy, 1969
metabromuron (<i>C. vulgaris</i>)	Pillay and Tchan, 1970
monuron (low rates, <i>Chlorella</i> sp. and <i>Chlamydomonas</i> sp.)	1972
neburon (low rates, <i>Chlorella</i> sp. and <i>Chlamydomonas</i> sp.)	Pillay and Tchan, 1970, 1972
PH-2846 (<i>C. ellipsoidea</i>)	Sumida and Ueda, 1973
propanil (low rates, blue-green algae)	Ibrahim, 1972
simazine (<i>Chlamydomonas eugametos</i>)	Vance and Smith, 1969

NEUTRAL EFFECTS

2,4-D (N_2 fixation)	Singh, 1974b
2,4-D (various algae)	Vance and Smith, 1969; Arvik et al., 1971; Torres and O'Flahery, 1976
2,4-D (<i>C. pyrenoidosa</i>)	Thomas et al., 1973
2,4,5-T (various algae)	Vance and Smith, 1969
atrazine (<i>Chlamydomonas reinhardtii</i> , heterotrophic growth)	Loeppky and Tweedy, 1969
atrazine (<i>C. vulgaris</i>)	Loeppky and Tweedy, 1969
barban (<i>Chlorella</i> sp.)	Cho et al., 1972
benzuride (green algae)	Bisiach, 1972
chloramben (<i>Chlorella</i> spp.)	Helling et al., 1971; Kratky and Warren, 1971
dalapon (<i>Chlorella</i> spp.)	Helling et al., 1971; Kratky and Warren, 1971
diphenamid (<i>Chlorella</i> spp.)	Thomas et al., 1973

Table XIV
Continued.

Herbicide	Reference
EPTC (<i>Chlorella</i> spp.)	Helling et al., 1971; Kratky and Warren, 1971; Thomas et al., 1973
fluormeturon (<i>Chlorella</i> sp., <i>Euglena</i> sp., heterotrophic growth)	Loeppky and Tweedy, 1969
MCPA (various algae)	Metting and Rayburn, 1979b
metabromuron (<i>C. eugametos</i> , <i>C. reinhardii</i>)	Loeppky and Tweedy, 1969
monuron (N ₂ fixation, following temporary inhibition)	DaSilva et al., 1975
nitralin (<i>Chlorella</i> spp.)	Helling et al., 1971; Kratky and Warren, 1971; Thomas et al., 1973
pyrazon (<i>Chlorella</i> spp.)	Helling et al., 1971; Kratky and Warren, 1971; Thomas et al., 1973
terbacil (<i>Chlorella</i> spp.)	Helling et al., 1972; Kratky and Warren, 1971; Thomas et al., 1973

India proved beneficial (Venkataraman, 1966). However, simultaneous inoculation of soil with *Nostoc* and *Azotobacter* increased oat yields in the Soviet Union by 34%, a value larger than the sum of separate inoculation trials (Shtina, 1957).

Greenhouse studies have demonstrated that algae inhibit the growth of tobacco (Engle and McMurtey, 1940), but promote growth of established citrus seedlings (Breazeale, 1929). Wakabayashi (1925) postulated that inoculation of cranberry bogs with algae might improve yields by increasing oxygen concentration in the root zone. Inoculation of tomato plants with *Tolypothrix tenuis*, in greenhouse trials, proved to increase the vitamin C content of the fruits to an extent comparable with different strains of *Azotobacter* (Aiyer et al., 1964). Also, lettuce and chilies fertilized with *Calothrix* were found to be more productive than non-algal controls (Dadhich et al., 1969).

ALGAE AS SOIL CONDITIONERS

Algae have been used as green manure on cotton fields in Tashkent (Kuchkarova, 1962; Tret'yakova, 1970), for reclamation of saline and sodic-saline soils in India (Singh, 1950, 1961), and to improve structure

Table XV
Effects of fungicides on algae in culture.

Fungicide	Reference
NEGATIVE EFFECTS	
captan (<i>Euglena gracilis</i>)	Lazaroff, 1967
captan (<i>Stichococcus hacillaris</i>)	Marton, 1973
ceresan (<i>Anabaena</i> sp.)	Venkataraman and Rajyalkshimi, 1972
dichlone and most other quinones (various algae)	Sikka et al., 1971; Zweig et al., 1972; Schwelitz et al., 1974
dichlorophen (<i>Chlorella</i> <i>pyrenoidosa</i>)	Gupta and Saxena, 1974
difolatan (<i>Westiellopsis</i> <i>prolifca</i> , <i>Tolypothrix tenuis</i>)	Gangawane and Saler, 1979
dithane (<i>S. bacillaris</i>)	Marton, 1973
hexacap (<i>Nostoc</i> sp., <i>W.</i> <i>prolifca</i>)	Gangawane and Saler, 1979
MBC (<i>W. prolifca</i>)	Gangawane and Saler, 1979
MBC (<i>C. pyrenoidosa</i>)	Carton, 1976
nabam (<i>Euglena gracilis</i>)	Lazaroff, 1967; Moore, 1970
nabam (<i>Anabaena</i> sp., <i>Chlorella</i> sp.)	Audus, 1970
sodium benzoate (<i>S. bacillaris</i>)	Marton, 1973
vapam (<i>E. gracilis</i>)	Moore, 1970
zinels (<i>Anabaena</i> sp., <i>Nostoc</i> sp.)	Venkataraman and Rajyalakshimi, 1972
POSITIVE EFFECTS	
difolatan (<i>Aulosira fertilissima</i>)	Gangawane and Saler, 1979
NEUTRAL EFFECTS	
ceresan (<i>Anabaena</i> spp., <i>A.</i> <i>fertilissima</i> , <i>Tolypothrix</i> <i>tenuis</i>)	Venkataraman and Rajyalakshimi, 1972
ethirimol (<i>C. pyrenoidosa</i>)	Teal, 1974
hexacap (<i>A. fertilissima</i> , <i>Calothrix</i> sp., <i>T. tenuis</i>)	Gangawane and Saler, 1979
MBC (<i>A. fertilissima</i> , <i>Calothrix</i> , sp., <i>Nostoc</i> sp., <i>T. tenuis</i>)	Gangawane and Saler, 1979
zineb (<i>A. fertilissima</i> , <i>Tolypothrix tenuis</i>)	Venkataraman and Rajyalkshimi, 1972

Table XVI
Effects of insecticides on algae in soil.

Insecticides	Reference
NEGATIVE EFFECTS	
lindane (diatoms in rice paddies)	Ishizawa and Matsuguchi, 1966
POSITIVE EFFECTS	
chlorpyrifos (blue-green algae in rice)	Sivasithamparam, 1970
diazinon (blue-green algae)	Sethunathan and MacRae, 1969
NEUTRAL EFFECTS	
carbaryl (blue-green algae in rice)	Ishizawa and Matsuguchi, 1966
parathion	Naumann, 1970b

in Mexico (Lewin, 1977) and central Washington state (Metting, unpublished).

In the manner prescribed by Singh (1950, 1961), for reclamation of "Usar" lands, artificial impoundments are made by constructing half meter earthen banks around an area of an acre or less. One or more species of *Microcoleus* (*M. cthonoplastes*, *M. vaginatus*) and *Scytonema* (*S. ocellatum*, *S. hofmanii*, *S. javanicum*) are the first algae to grow up on loose soils following the first seasonal rains in June. *Porphyrosiphon notarisii* takes their place on hard, compacted soils. By August, puddled soils are dominated by one or more species of *Scytonema*, with germination of the resting spores of any of the following algae also taking place at this time: *Nostoc commune*, *N. muscorum*, *N. linckia*, *Camptylonema lahorensis*, *Cylindrospermum licheniforme*, *C. muscicola*. This synusium of dinitrogen-fixers dominates the wet soil throughout the duration of the rainy season (August–November). In most soils, *N. commune* is clearly the dominant alga, however, if conditions are such that soils in the impoundments become waterlogged for any length of time, *Aulosira fertilissima*, *Anabaena ambigua*, *A. fertilissima*, *Cylindrospermum gorakhporensis*, or *Wolleea bharadwajae* may become dominant. After one or two years, the pH is reduced to 7.6 from 9.5, the water-holding capacity is increased by as much as 40%, and exchangeable Ca is increased 20–30% (Singh, 1950, 1961).

Natural algal succession in sugarcane, maize, and grassland soils is also important as a green manure. In India, sugarcane is grown on well-drained silt loam, or sandy loam soils which are seldom waterlogged. Following the first monsoon rains, *Microcoleus cthonoplastes*, *Porphyrosiphon notarisii*, and *Scytonema ocellatum* appear. This association is

Table XVII
Effects of insecticides on algae in culture.

Insecticide	Reference
NEGATIVE EFFECTS	
benzene hexachloride (<i>Aulosira fertilissima</i> , <i>Plectonema</i> sp.)	Singh, 1973
carbaryl (<i>Chlorella pyrenoidosa</i>)	Christie, 1969
DDT (<i>Anabaena</i> sp.)	Czeczuga and Gierasimow, 1973
DDT (<i>Anacystis nidulans</i>)	Batterton et al., 1972
DDT (<i>Chlorella</i> spp.)	Södergren, 1968, 1971; Czeczuga and Gierasimow, 1973
dieldrin (<i>Anacystis nidulans</i>)	Batterton et al., 1971
endrin (<i>A. nidulans</i>)	Batterton et al., 1971
lindane (blue-green algae)	Singh, 1973
POSITIVE EFFECTS	
lindane (<i>Protococcus</i> sp.)	Ukeles, 1962
NEUTRAL EFFECTS	
DDT (<i>C. pyrenoidosa</i>)	Christie, 1969
DDT (<i>Chamydomonas reinhardii</i>)	Morgan, 1972
DDT (<i>C. reinhardii</i> , <i>Euglena gracilis</i>)	Mosser et al., 1972
diazinon (<i>Aulosira fertilissima</i> , <i>Cylindrospermum</i> sp.)	Singh, 1973
endrin (<i>A. fertilissima</i> , <i>Cylindrospermum</i> sp.)	Singh, 1973
malathion (various algae)	Torres and O'Flaherty, 1976
malathion (N ₂ fixation)	DaSilva et al., 1975
malathion (<i>C. pyrenoidosa</i>)	Christie, 1969
malathion (<i>E. gracilis</i>)	Moore, 1970
parathion (various algae)	Gregory et al., 1969
parathion (<i>E. gracilis</i>)	Moore, 1970

superceded first by *Aphanothece pallida*, *Nostoc commune*, *N. muscorum*, and *N. linckia*, and finally by *Cylindrospermum licheniforme* and *C. maius* on dryer soils, or by *Aulosira fertilissima* on more moist soils. Soils in which maize is grown support *C. licheniforme*, while grasslands are variously dominated by any combination of *P. notarisii*, *S. ocellatum*, *S. hofmanii*, *C. lahorensis*, *C. licheniforme*, *C. maius*, or *C. muscicola* (Singh, 1961). For a complete listing of blue-green algal species in India, see Raju (1972).

Table XVIII

Effects of fumigants and pollutants on algae in soil (all effects are negative).

Fumigant	Reference
allyl alcohol (indigenous populations)	Nauman, 1970a, 1970b, 1971, 1972
dazomet (indigenous populations)	Nauman, 1970a, 1970b, 1971, 1972
formalin (indigenous populations)	Nauman, 1970a, 1970b, 1971, 1972
methamsodium (indigenous populations)	Nauman, 1970a, 1970b, 1971, 1972
Pollutant	
Fe, S wastes	Kildema and Roos, 1977
PCB's	Wright, 1978
styrene (phenylethylene)	Munjko and Brbic, 1977

The use of large quantities (1–5 kg/ha) of *Chlamydomonas mexicana* Lewin on recently tilled soils in arid regions of Mexico and the American southwest has been proposed as a means of increasing fertility and improving structure by binding clays and preventing formation of a hardpan (Lewin, 1977). Preliminary observations suggest that up to 90% of the photosynthate produced by the alga, under ideal conditions, is converted to extracellular biopolymer (Fogel et al., 1976), and that depending on previous climatic and edaphic conditions, yields of cotton and potatoes are improved by 5–15%. After 3–4 weeks, the initial inoculum grew to 50–200 kg/ha, water savings were up by as much as 35–45%, erosion was reduced, the salt table was lowered, and incidence of root rot was reduced (Lewin, 1977).

THE RHIZOSPHERE EFFECT

Crops also influence algae. It has been pointed out above that diversity and numbers of algae can be increased or decreased as a result of farming practices. Rhizosphere effects on soil algae vary with the species of vascular plant (Starkey, 1938; Shtina, 1956; Aleksakhina, 1972). Positive rhizosphere effects have been noted for diatoms with *Artemesia* Linn. and *Lasiagrostis* Link. and for diatoms and blue-green algae with roots of mangel (Katznelson, 1946), sorghum, cotton, and wheat (Gonzalves and Yalavigi, 1960). The effects noted by Gonzalves and Yalavigi (1960) were greatest at anthesis, at which point diversity of green and blue-green algae approximated that obtained in root-free soil amended with farmyard manure or $(\text{NH}_4)_2\text{SO}_4$. A negative rhizosphere effect on algae was reported by Hadfield (1960) for the tea bush and by Rauatt et al. (1960), for wheat.

Table XIX
Instances of uptake and metabolism of pesticides by algae in culture.

Pesticide	Reference
2,4-D (<i>Chlorella pyrenoidosa</i>)	Wedding and Erickson, 1957
DDT (<i>anacystis nidulans</i> , <i>Scenedesmus quadricauda</i>)	Gregory et al., 1969
dieldrin (<i>C. pyrenoidosa</i>)	Wheeler, 1970
etherimol (green algae)	Teal, 1974
ioxynil (green algae)	Fletcher et al., 1970
lindane (<i>Chlorella vulgaris</i> , <i>Chlamydomonas reinhardtii</i>)	Sweeney, 1969
malathion (<i>C. pyrenoidosa</i>)	Christie, 1969
MCPA, MCPB (green algae)	Fletcher et al., 1970; Kirkwood and Fletcher, 1970
parathion (<i>C. pyrenoidosa</i>)	Mackiewicz et al., 1969; Zuckerman et al., 1970
propanil (various algae)	Wright, 1972; Wright et al., 1977
propanil (<i>Chlorococcum aplanosporum</i>)	Sharabi, 1969
simazine (<i>Chlorosarcina</i> sp.)	Kruglov and Paromenskaya, 1970

SOIL ALGAE AND PESTICIDES

A number of studies have been undertaken to assess the influence of pesticides, both insecticides and herbicides, on growth of soil algae. Results have been variable, with inhibition and stimulation of growth, or no effect on growth having been reported from in situ and culture experiments. Interpretation of these results must however, be considered in light of a number of points. Factors such as soil variability, farming practices, plant cover, and formulation have been shown to influence the effect on non-target microorganisms of pesticides and, therefore, extrapolation to field situations of results obtained in culture must be guarded (Cullimore, 1971; Butler, 1977; Anderson, 1978; McCann and Cullimore, 1979).

Of the three major groups of pesticides commonly employed in agriculture, at least a few studies have been conducted in both soil and laboratory culture, with the exception of fungicides, for which in situ work has not yet been undertaken. In Tables XIII through XVIII are collected the results of experiments in which a negative, positive, or neutral influence of herbicides, fungicides, insecticides, soil fumigants, or pollutants on soil algae was demonstrated. By including results of culture work with species of *Anabaena*, *Anacystis*, *Chlamydomonas*, *Chlorella*, and *Eu-*

glena from aquatic habitats, more can be said of the possible influence of pesticides on closely related edaphic forms.

In general, herbicides inhibit the growth and reproduction of soil algae, although negative results observed in the laboratory are often more pronounced than in soil. For example, propanil was less inhibitory to algae in soil than in culture (Sharabi, 1969; Ibrahim, 1972; Wright et al., 1977). Also, when presented together, pesticides may be less or more toxic to algae than when presented separately (Arvik et al., 1971). The influence of a particular chemical may also be determined, in the laboratory, by the degree of purity of the algal culture (Wright, 1978; Metting and Rayburn, 1979b).

In addition to being inhibited or stimulated, many algae absorb and/or degrade pesticides (Vance and Drummond, 1969; Wright, 1978). Examples are included in Table XIX. Uptake is strongly influenced by temperature and pH (Wedding and Erickson, 1957; Fletcher et al., 1970). No evidence has accrued with respect to the possibility that absorption of a pesticide by algae in situ might alter its toxicity or enhance its degradation.

Culture experiments have been quantified by various methods in addition to direct estimation of biomass. These include paper disc assays on soil or agar media (Pillay and Tchan, 1969, 1970, 1972; Kruglov and Paromenskaya, 1970; Cullimore, 1975; Kruglov and Kwiatkowskaya, 1975; Wright, 1975a, 1975b), motility assays (Lazaroff, 1967), analysis of thin layer chromatograms (Helling and Kaufman, 1970; Helling, 1971; Helling et al., 1971), agar plate assays (Ikawa et al., 1969; Thomas et al., 1973), and analysis of bioluminescence by *Photobacterium* Beijernick sp., the intensity of which is proportional to algal photosynthetic oxygen production (Tchan et al., 1977; Tchan and Chiou, 1977). In addition, the influences of herbicides on algae have been used as bioassays for their potential use in weed control (Atkins and Tchan, 1967; Addison and Bardsley, 1968; Krattky and Warren, 1971; Cullimore, 1975; Matorin et al., 1975).

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