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MICROCLIMATE AND THE RESPONSE OF PLANTS TO NITROGEN

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INTRODUCTION

What elements of microclimate might be expected to influence the response of plants to nitrogen fertilization? Do they act directly upon the supply and delivery of the nitrogen or indirectly upon the plant growth?

If we define the prime intent of agriculture as the capture of sunlight by photosynthesis, then foremost among the elements of microclimate must be the light interception by the array of leaves within the canopy. Large well-fertilized vegetative plants with high populations result in competition for light that leads to mutual shading of the leaves and immediate problems of nitrogen reductase.

The canopy architecture affects the turbulent exchange of carbon dioxide and water vapor, both of which are the basic raw materials for photosynthesis. Chlorophyll must be present for photosynthesis in plants. Morever, chlorotic, nitrogen-deficient plants have a higher reflectance, hence, lower potential photosynthesis.

Enzyme systems, such as carboxylase which reduces carbon dioxide, depends on the supply of nitrogen as well as a number of minor elements such as molybdenum, iron, and zinc. The transpiration stream is a function of the net radiation and the turbulent exchange from the canopy. The evaporation cools the leaf, and the transpiration stream from soil to root through the plant serves for the mass transport of the nitrate. The respiration rate induced by the leaf temperature governs gross photosynthesis.

The rate of mineralization of the various nitrogen forms in the soil are temperature and moisture dependent. Translocation and storage of the photosynthates prior to harvest are all light, temperature, and moisture dependent. Where then, can we make a beginning?

SOME LIMITING FACTORS OF NITROGEN REDUCTASE

Recent attention to plant morphology and stand geometry in relation to nitrogen has paid handsome dividends such as the spectacular yield increase of the new IRRI rice and the CYMMT wheat (Chandler, 1969; Donald, 1969).

The use of genetic dwarfs to permit high nitrogen fertilization without lodging has been said to be the greatest single promise for continued upward displacement from the yield plateau. Erectophile leaf habit, high leaf area indices, and high plant populations are used to engineer plants for maximum photosynthetic efficiency under high light conditions with non-limiting nutrition and irrigation. (Duncan, W. G., 1971; Williams, et al., 1968; Fagade, et al., 1971). The recently discovered high potential efficiency of carbon fixation by tropical grasses with their 4-carbon pathway, lack of photorespiration, and unique leaf design has caused a renewed flurry of interest in the possibilities of these tropical species as opposed to the more conventional temperate latitude plants. (Brown & Gracen, 1972; Fery & Janick, 1971; Krenzer & Moss, 1969; Hesketh & Baker, 1967; Bull, 1969.)

The principle action of canopy architecture seems to be in the decreased nitrogen reductase activity under mutual shading which results from high plant populations and greater vegetative growth from increased nitrogen fertilization. Most of the soil nitrogen is assimilated by the plant (except for paddy crops) in the form of nitrate which must be reduced to ammonium ion within the plant prior to transformation into amino acids and protein. High plant nitrate levels are found in crowded plants (mutual shading) under low light conditions (cloudy days) with adequate soil nitrogen and soil moisture levels. (Hageman & Flesher, 1960; Hageman, et al., 1961; Earley, et al., 1966; Beevers, et al., 1965; Harper & Paulsen, 1969; Croy & Hageman, 1970.) The increased use of sorghum in Hawaii as a field crop brings with it concern over the development in the plant of nitrate levels toxic to animals when high nitrogen fertilization induces rank vegetative growth, with mutual shading. Toxic levels can develop within a few days, particularly if temperature remains high (George, et al., 1971; Murphy & Smith, 1967).

The precise cause for the yield limitation from the competition induced by high plant populations though still disputed, has been variously assigned to reduced exchange of carbon dioxide and heat, increased water use, and mutual shading (Hunt, et al., 1967; Szeicz, et al., 1969; Rumawas, et al., 1971; Brown & Rosenberg, 1971; Lemon, et al., 1971). Nitrogen status and leaf color are correlated with chlorophyll content. The increased reflectance from Nitrogen chlorosis is small, but it does reduce the net radiation (Thomas & Oerther, 1972; Sinclair, et al., 1971).

The preferential assimilation of ammonium by paddy crops suppresses nitrate utilization since ammonium inhibits the first step of nitrate reduction (Shen, 1969).

The response of reductase to molybdenum is rapid and drying of the soil surface layers can induce a temporary molybdenum deficit (Mattas & Pauli, 1965). Even mild water stress can cause decreased reductase activity, apparently in an attempt to reduce plant energy requirements by decreasing the rate of nitrate accumulation (Huffaker, et al., 1970).

The rate of carbon dioxide fixation by nitrogen deficient leaves is low, owing to an apparent increase in the mesophyll resistance to carbon dioxide transfer. However, the normal rate of fixation was restored within 4 days by the addition of nitrate to nitrogen-starved plants (Ryle & Hesketh 1969; Nevins & Loomis, 1970). The rate of carbon fixation also depends on the enzyme systems for carboxylase activity. Light levels, age, acclimatization, and zinc deficiency play parts in the adjustment of the response rate even though nitrogen may be adequate. (Huffaker, et al., 1970; Bowes, et al., 1972; Hart & Lee, 1971; Beuerlein & Pendleton, 1971; Treharne, et al., 1968; Jyung, et al., 1972).

The response to light factors can be even more complex, since the photoperiod of even tropical species interacts with temperature to induce differentiation and flowering which disrupts the normal patterns of vegetative growth (Miller, et al., 1968). Reduction in photosynthesis in response to magnesium seems to occur only when the actual magnesium deficiency symptoms are visible (chlorophyll deficiency). Potassium shortage on the other hand, reduces photosynthesis long before the appearance of potassium associated symptoms, apparently in response to a potassium-induced reduction in stomatal openings (Peaslee & Moss, 1966).

The interaction among canopy architecture, light intensity, nitrogen fertilization, and plant yield, particularly of protein, is intimately associated with the level of nitrogen reductase, though a host of other factors can induce limitations.

SOIL TEMPERATURE

The effects of soil temperature can be direct as in the effect on the rate of mineralization of soil organic matter or indirect as in the effect upon the flux of water through the plant root and the associated nitrate carried in solution. Mineralization of proteins and related organic matter by enzymatic hydrolysis degrades the compounds into ammonia and carbon dioxide. Many soil organisms can accomplish this, hence, fresh organic matter undergoes rapid decomposition (Harmsen & van Schoreven, 1955). The older and more complex nitrogen compounds in the soil organic matter can also be oxidized heterotrophically to nitrate (Eylar & Schmidt, 1959). The activity of these heterotrophic nitrifiers persists to temperatures of 98.6 to 122°F, temperatures which inactivate the Nitrosomonas and Nitrobacter nitrification of ammonia (Etinger-Tulczynska, 1969). The ammonification of organic matter can occur in soils dried well below the 15-bar point. Water is therefore, seldom limiting, though no ammonification occurs in completely air dry soils (Robinson, 1957). The critical threshold water content for the decomposition of many plant residues is 80 percent relative humidity, or about 200 bars (Bartholomew & Norman, 1947).

Low temperatures inhibit nitrification more than ammonification. Nitrobacter is more sensitive to low temperature than Nitrosomonas. The optimum for nitrification is 89.6°F, with inhibition at 104°F. Though no absolute minimum seems to occur, the most rapid decrease occurs between 44.6 and 59°F (Tyler, et al., 1959; Frederick, 1956; Anderson & Boswell, 1964; Anderson, et al., 1970). Though nitrification also continues till the soil moisture is reduced below 15 bars, little reaction occurs at moisture levels appreciably below this (Justice & Smith, 1962).

In Hawaii, where the temperatures are governed by the surrounding sea, the average water temperature is 75°F, with a range from 72 to 78°F in season. The dry adiabatic decrease of 5.4°F for the first 2,000 feet, and then of 3°F/1000 feet suggests that critical temperatures for nitrification occur only for elevations above 2,000 feet.

The effect of root temperature on water flux is very large, since root temperatures near 50°F sharply reduce intake and can cause temporary wilt and reduced growth even at 60°F. The activation energy for water flow through roots indicates a metabolic control in contrast to physico-chemical control through the stem (Jensen & Taylor, 1961; Unger & Danielson, 1967; Tew, et al., 1963). Sugarcane roots are sufficiently affected by temperatures of 55.4 to 57.2°F to reduce growth and water use (Mongelard & Mimura, 1971; Nielsen & Humphries, 1966). The use of vapor barrier mulches in Hawaii has a peculiar history. Though the containment of the fumigant is a major intent today, the mulches which increase soil temperature, instigate a complex interaction which generally stimulates plant growth, in part through changes in nitrate levels beneath the mulch (Black & Grebb. 1962: Ekern. 1967; Adams, 1970).

AIR TEMPERATURE EFFECTS

The temperature of the aerial parts of the plant has great bearing on the growth response, too. Increased respiration reduces net photosynthesis as higher temperatures occur and forms an important predictor of the consequences of changes in leaf metabolism and physics on the net photosynthetic production (Beevers, L. & Hanson, J. B., 1964; Waggoner, P. E., 1969).

Though maize is a tropical grass, and adapted to a higher optimum temperature, different races still show different responses in photosynthesis and leaf growth to temperatures (Duncan, W. G. & Hesketh, J. D., 1968; Treharne, K. J. & Cooper, J. P., 1969). The reason for this temperature response seem to stem, in part from the importance of the translocation of the photosynthate away from the chloroplasts, if high rates of carbon fixation are to be maintained (Hartt, C. E., 1963). Certainly translocation is temperature sensitive though the activation energy suggests that an activated-diffusion type of mechanism must prevail (Whittle, C. M., 1964).

Many tropical species are subject to chilling injury if night temperatures fall to 10 to 15°C (50 - 60°F). The reduced growth and chilling injury is accompanied by changes in the nitrogen metabolism, with protein synthesis increased in the effort to recover from the chill. However, reduced chlorophyll synthesis, offset by carboxin and reduced amylotic activity with failure to translocate starch, which can be offset by giberellic acid, have been demonstrated to also affect the chilling response (Schmidt & Blaser, 1969; Omran, et al., 1971; Karbassi, et al., 1972; Karbassi, et al., 1971; Sachs, et al., 1971). Nitrate reductase activity in temperature grasses is progressively reduced by high air temperatures of 105.9 - 109.4°F (Onwueme, et al., 1971). The ability of some desert species, with the C-4 carbon cycles, to maintain photosynthesis at temperatures of 111.8° to 122°F has been recorded, but the accompanying heat stability of the enzyme systems has not been specified (Bjorkman, et al., 1972). Nitrate supply, its transport to and through the plant, its reduction within the plant, and enzymatic effects on metabolic processes are all temperature sensitive. Low temperatures create a marked reduction in the growth of tropical crops even at temperatures far from freezing.

Soil temperature governs the pool of available nitrate as well as the rate of mass flow within the transpiration stream. Air temperature determines the rate of respiration, hence, the level of net photosynthesis. There are, however, direct effects upon nitrogen metabolism, since the level of nitrogen reductase is temperature sensitive. The peculiar chilling injury of tropical crops stems in part from disruption of the nitrogen metabolism.

SOIL MOISTURE EFFECTS

The bulk of the readily available pool of soil nitrogen is in the nitrate form, hence, it is particularly mobile. Essentially all of the nitrate is dissolved in the soil water and is free to move with it (Viets, 1967). The fate on nitrogen fertilizers applied to the soil is a feature of great current interest, since it constitutes a potential pollution hazard to ground waters (Pratt, et al., 1972, Green & Young, 1970, Kohl, et al., 1971; Viets, 1971). The closing of the nitrate cycle still has a number of missing links. Particularly sketchy is the manner in which the nitrates suffer denitrification in the oceans to maintain the large nitrogen content of the air (Gupta, 1969). Fertilizer nitrogen, in addition to being absorbed by the crop, may meet a number of other fates (Power, 1968). Anhydrous or aqua ammonia are sorbed initially on the clay minerals and may be fixed within the clay lattice (Nelson, 1953; Dow, et al., 1953). Losses as gaseous ammonia can occur and may be as great as 60 percent from anhydrous application or 10 to 20 percent from the aqua form (Kresge & Satchell, 1960; Henderson, et al., 1955; Humbert & Ayres, 1956, Humbert & Ayres, 1957). These gaseous transformations may not be a complete loss, for uptake of ammonia by leaves from the air has recently been confirmed (Hutchinson, et al., 1972; Porter, et al., 1972).

Under temperatures which prevail in Hawaii, rapid conversion of the ammonia into nitrate generally occurs within the soil at the sites of anion absorption (Lees & Quastel, 1966). Urea is rapidly hydrolyzed into ammonium carbonate and subsequently nitrified. The urease activity in the soil appears to be divided into two components, the microbial urease and urease sorbed on the soil colloids (Paulson & Kurtz, 1970). Urea hydrolysis proceeded at about the same rate in waterlogged soils as in soils kept at 1/3-bar moisture. Volatization loss of ammonia was slightly greater at 1/3 bar than under waterlogged conditions (Delaune & Patrick, 1970). The loss by volatilization at high soil or water temperatures from surface applied urea can be reduced by sulfur coats which reduce the rate of dissolution of the urea (Allen, et al., 1971).

Soil fumigants, a number of fungicides, and several compounds, such as N-serv, reduce the action of nitrifiers and delay the transformation of ammonia into nitrate (Goring, 1962; Smith, 1963; Tam, 1945; Dubey, 1969).

One import aspect of nitrification is the development of residual soil acidity due to excess bases being removed by the crop and the fate of the residual fertilizer (Pierre, 1970). The nitrate remains almost exclusively in the soil water and is subject to ready movement by miscible displacement. Relatively minor anion exchange of nitrate occurs in red latosols* and the elution curve for chloride, bromide, and nitrate are similar (Singh & Kanehiro, 1969; Miller et al., 1965; Berg & Thomas, 1959). Both osmotic and matrix suction forces are present where hygroscopic fertilizer materials are banded and a complex pattern of diffusion to the salt band and subsequent dissolution and capillary movement downward of the nitrate occurs (Burns & Dean, 1964). Similarly, the evaporation zone near the soil surface develops a complex circulation of salt and water transport which involves vapor phase transfer of the water and salt accumulations at the actual vaporization site within the soil (Gardner & Hanks, 1966; Qayyum & Kemper, 1962). Water is essential to the uptake of the soil nitrate by plants. The transpiration stream sweeps the nitrate to the root by mass action (Barber, Walker & Vasey, 1963). Attempts to untangle the skein of water uptake, nutrient uptake, plant turgor, plant transpiration, and growth rate continue. Water uptake and root distribution patterns suggest that roots have a significant impedance to water flow even under moist conditions (Molz, 1971).

Even under controlled studies, the integrated effect of soil water conditions on transpiration and plant growth are devious, but suggest that growth rate decreases sharply with soil water stress from 0 to 1 bar (Rawitz, 1969). The method of water application, sprinkler, furrow, flood, drip, or subsurface, determines the pattern of water distribution as well as the pattern of nitrate movement within the soil profile. Sprinkler irrigation is more effective in salt leaching than furrow flood applications (Robinson & McCoy, 1967; Robinson, et al., 1968; Goldberg & Shmueli, 1970; Brandt, et al., 1971).

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*now classified as oxisol, ultisols or inceptisols

Crop recovery of applied fertilizer nitrogen often is quite low, perhaps only 25 percent but the critical factors are the yield responses, for the full cycling of the applied fertilizer within the soil may require a period of years (Pratt, 1972). Losses in percolate through the profile, however, present a pollution hazard, through recovery in part by recycled irrigation waters. A growing crop forms an almost completely effective nitrate sink when soil temperatures are not restrictive (Terman & Brown, 1968; Ekern, 1970; Takahashi, 1968). Though the use of commercial nitrogen fertilizer has been the major energy input into mechanized agriculture (Odum, 1967) it accounts for but 10 percent of the world's soil nitrogen fertilization.

Nitrogen fixing plants play a large part in the usual cycle (Stewart, 1967) Under the water logged conditions of paddy culture, blue-green algae can fix nitrogen to maintain subsidence levels of agriculture where legumes cannot be used. The temperature regime in the shallow waters of paddies favors rapid algal growth and promotes nitrogen fixation (Rose & Chapman, 1968; Chapman, 1969; Lourance & Pruitt, 1971). Such algal fixation is not confined to water filters, but occurs in soil crusts of dry soils as well (Cameron & Fuller, 1960)

SUMMARY

Among the many microclimatological parameters which govern plant growth in response to nitrogen fertilization are; light quality and intensity which control photosynthesis but also regulate the plant nitrogen pool through control of nitrate reductase, net radiation which controls the transpiration stream responsible for transport of nitrate to and through the plant; plant temperature which regulate the rate of many physiochemical and metabolic systems within the plant which are responsible for the translocation and transformation of the initial photosynthates into harvestable products; soil temperature which regulates the microbial activity essential to mineralization of the soil nitrogen storage forms, and soil moisture which regulates the transport of nitrogen within the soil.