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Environmental Factors Affecting Plant Productivity

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Abstract

Plants are affected by the environment during all phases of growth and development. The impact of selected environmental factors on range plant productivity is discussed with emphasis on water, temperature, light, atmosphere, nutrients, fire, and grazers.

Key Words: range, plant, productivity, stress, environment, water, temperature, light, atmosphere, nutrients, fire, grazers

Introduction

From the time a plant breaks dormancy, begins vegetative growth, flowers, produces fruit, and goes into a dormant state, many environmental factors can act singly or interact to affect productivity. The importance of the topic is shown by the accumulation of numerous textbooks, reviews, and technical articles that address plant autecology, physiological ecology, and community ecology, but only a portion of the literature could be reviewed in this paper. Lewis (1969) in his review on range management in an ecosystem framework delineated controlling factors (climate, available organisms, and geologic materials) and dependent factors (vegetation, consumers, decomposers and transformers, soil, and microclimate). Daubenmire (1974) related plant autecology to soil, water, temperature, light, atmospheric, biotic, and fire factors. Both stressed that numerous factors operate on organisms simultaneously, and species and ecotypes do not always respond to stimuli in a like manner. Several authors have also discussed varying responses to environmental factors – i.e., water, temperature, light, and nitrogen – exhibited by plants with the C_3 and C_4 photosynthetic pathways (Christie and Detling 1982, Caldwell 1985a, Ehleringer 1985). Environmental factors selected for this discussion on plant productivity include water, temperature, light, atmosphere, nutrients, fire, and grazers.

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Water

Water is required by all living organisms. Plants can be stressed by lack of moisture as well as an excess of moisture. Brown (1977) reported that the availability of water was the most important environmental factor limiting growth and survival of range plants. He indicated that water deficits developed in plant tissue when rate of transpiration exceeded that of water absorption. Risser (1985) reported that the high positive correlations found between available soil moisture and forage production were related to a decrease in net photosynthesis as leaf water potentials decrease. Hsiao (1973) presented a sequence of events that occurred when a plant was growing in a moist situation and then encountered moisture stress. A slowing down of root and leaf growth was listed first. In his discussion on the relation of water stress to long-term growth and yield, he elaborated on the fact that cell growth was generally more sensitive to water stress than was stomatal opening and CO_2 assimilation. He further emphasized that mild moisture stress may not affect photosynthesis, but it can reduce the development of leaf surface area. Whether the reduction in leaf surface area affects dry matter yields is dependent upon whether leaf area is limiting the crop's assimilation of CO_2. Sensitivity of dry matter yield to stress should be greater in a growing crop with a low leaf area index (leaf area per unit land area) that is limiting the crop's assimilation of CO_2 than in a crop with a high leaf area index that is not limiting assimilation of CO_2.

Slatyer (1974) reported that the most obvious effects of prolonged water stress on shoot development were reduced internode length and reduced leaf size. He stated that effects on leaf size, rate of leaf expansion, and rate of appearance of new leaves had profound effects on total dry matter production. Photosynthetic area increased less rapidly, and also stomata tended to become nonfunctional more quickly in older compared to younger leaves.

Slatyer (1974) summarized the effects of water stress on annuals as: (1) reduced leaf size and internode length, (2) stunted tops of plants, (3) suppressed root growth in proportion to shoot growth, (4) delayed time of flowering and fruit set although they occurred at similar ontogenetic stages as in well watered species, (5) reduced seed num-

ber, size, and viability, and (6) halted growth and development with severe stress, followed by death.

Slatyer indicated that a similar general effect of reduced leaf size and internode length could be expected on shoot development of perennial grasses. Root growth, however, could continue if roots were growing in moist soil. This continued growth resulted from the fact that root growth was controlled more by local levels of soil-water potential than by mean plant-water potential. With increasing stress, reproductive development may be delayed, and floral initiation may not occur. With severe stress, shoot dieback may occur, but new tillers will develop from basal buds when water becomes available.

Woody evergreens respond similarly to perennial grasses; shoot growth may cease, but root development will occur in moist soil (Slatyer 1974). The pattern of shoot development may, however, be affected for long periods where growth is mainly seasonal and is based on development of over-wintering buds. Water stress during bud development can affect subsequent vegetative and reproductive shoot development. Slatyer suggested that the number of leaves and flowers will be controlled by water stress during bud development; but leaf size, shoot length, amount of fruit set, and final seed size may be more influenced by water stress during the post winter period.

Excess moisture is tolerated by some plants but not by others. One has only to look at the ecotones that occur between stands of big sagebrush (*Artemisia tridentata*) and silver sagebrush (*Artemisia cana*) or to look at the death of some plant species in mountain meadows following flooding to see the impact of excessive water on plant productivity of some species. Ganskopp (1986) noted that several workers found excessive soil moisture detrimental to big sagebrush (U.S. Dept. Agr. Forest Serv. 1937, Branson 1956, Vallentine 1980), and others have speculated that anaerobic conditions in some soils prevent successful colonization of big sagebrush (Fosberg and Hironaka 1964). In flooded environments, oxygen is absent or more often in short supply, and the normal exchange of gasses from roots to soil is frequently disturbed (Feldman 1984). Kozlowski (1984) reported that flooding rapidly depleted soil oxygen, altered plant metabolism, and thereby inhibited growth. He indicated that flood tolerance varied widely among plant species, cultivars, and ecotypes and was associated with both morphological and physiological adaptations.

Temperature

Scientists have long recognized the importance of temperature in regulating rates of physiological processes and influencing growth and development of plants. Larcher (1980) stated that sufficient but not excessive heat is a basic prerequisite for life. Each vital process is restricted to a certain temperature range and has an optimal operating temperature on either side of which performance declines. Laude (1974) stated that temperature response is conditioned by the level of other factors of the environment. Two examples are the associations of temperature with moisture and radiant energy with temperature.

Cooper and Tainton (1968) reported that the optimum temperature for growth (dry matter increase or relative growth rate) occurs between 20° and 25°C for most temperate Festucoid (C_3) grasses. Growth rate drops rapidly below 10°C, but some growth occurs at 5°C, and the plant remains healthy. Growth is reduced above 25°C and may cease above 30-35°C, even with adequate soil moisture. Sub-tropical, non-Festucoid (C_4) grasses have an optimum of 30-35°C and grow extremely slow, if at all, at temperatures below 10-15°C. Exceptions occur in some species with optimum temperatures shifting according to local conditions (Noble 1980).

Berry and Bjorkman (1980) reported unequivocal evidence that inhibition of whole leaf photosynthesis by high temperature is caused by a disruption of the functional integrity of the photosynthetic apparatus at the chloroplast level. They also reported that dark respiration is more heat resistant than photosynthesis since nearly complete inhibition of photosynthesis occurs before any inhibition of dark respiration or other symptoms of high temperature injury can be detected in leaf tissue. Levitt (1980) stated that when high temperature was the primary stress, a water deficit was induced which subsequently caused mineral nutrient deficiency.

Cold temperatures can affect plant productivity by delaying initiation of growth in spring, restricting water movement to roots, decreasing permeability of the membrane on the root surface, and delaying opening of stomata on a daily basis, thereby reducing the duration of daily photosynthesis. Freezing temperatures can also injure and kill plants. Smith (1964) reported that winter injury and death of forage plants is a major hazard of grassland farming in many areas of the world; mortality occurred frequently where below freezing temperatures prevail for long periods.

Winter injury can result from low temperature, smothering, and desiccation (Smith 1964). Soil or snow cover may provide some insulation for crowns of plants. Temperatures alternating above and below freezing can cause damage through rapid freezing of plant cells, deacclimation or decrease in frost hardiness, and frost heaving.

Burke et al. (1976) also reported that freezing injury is a major cause of crop loss and that low temperature is reputedly the single most limiting factor to natural plant distribution. They stated that stresses of late spring and early fall frosts, low mid-winter minima, and rapid temperature changes cause various types of injury directly and indirectly associated with freezing of water in plant tissues. Injuries include crown kill in winter cereals, biennials, and herbaceous perennials; sunscald on thin-barked tree species; winter burn to evergreen foliage; blackheart and frost cracking in xylem of trees and shrubs; blossom kill; death of buds and bark in plants which lose hardiness rapidly during transient warm spells in winter; and outright death of tender annuals. Low temperature responses of most plants appear to fall between the 2 extremes of either being killed at the moment they freeze or tolerating extremely low temperatures (-196°C) in midwinter. Plant responses and freezing resistance, however, may change markedly with season and stage of plant growth.

Burke et al. (1976) stated that plants varied in their ability to tolerate ice crystal formation in tissues. Some became acclimated extensively in response to endogenous factors and the environmental factors of temperature and

day length. Some acclimated only a few degrees, while others did not acclimate at all. Smith (1964) indicated that hardiness developed most rapidly with shorter days and decreasing temperatures, and hardiness could be retarded by warmer temperatures accompanied by abundant soil moisture. Factors reducing plant vigor such as defoliation, disease, and lack of nutrients all effectively reduced acclimation (Smith 1964).

Smith (1964) reported that winter injury was usually more serious in a stand of old plants than in a stand of younger plants because: (1) old plants are likely to be weakened by invasions of disease and insects, (2) the fertility level of soil under an old stand is likely to be limiting, and (3) older stands have fewer plants per unit area than young stands. He indicated that evidence of injury to forage plants becomes apparent as growth begins in the spring. Injured plants begin growth slowly, are yellowish in color, and may have only a few stems per plant. Time is required for healing of tissue if plants are going to survive and regain vigor.

Winter kill has been reported for several shrub species growing on rangelands. These include mountain big sagebrush (*Artemisia tridentata* subsp. *vaseyana*) (Hanson et al. 1982), fourwing saltbush (*Atriplex canescens*) (Van Epps 1975), bitterbrush (*Purshia tridentata*) (Jensen and Urness 1979), and snowbrush (*Ceanothus velutinus*) (Stickney 1965).

Light

Photoautotrophic higher plants are dependent on light for survival (Smith 1982). The supply of light to an area of land is the most reliable environmental resource for plant growth since cloud cover causes the only serious variation in light climate at any point on the surface of the earth (Harper 1977). Light varies in intensity, duration, quality, and angle of incidence in both daily and annual cycles. Decreased light can become a limiting factor to plant growth when shading occurs; one major effect of shade is to slow the rate of photosynthesis relative to respiration (Harper, 1977). Thus, even an efficiently photosynthesizing plant may not grow if its respiratory burden becomes too large.

Solar radiation capture by individual plants is a function of several factors including leaf size, angle of display, pubescence, age, and physiological condition (Risser 1985). Since leaf surfaces are primary radiation interceptors, the amount of leaf surface is closely related to rate of growth in forage plants. Maintenance of a high leaf area index is very important for sustaining maximum growth rate. Broughman (1956) suggested that maximum growth results when leaves are sufficient to intercept 95% of the incoming solar radiation. Donald (1961) referred to an optimum leaf area index where every leaf was making a positive contribution to increased dry weight. As leaf area per plant increased beyond this optimum, crop growth rate began to decline. Harper (1977) suggested that a plant population growing within an environment of limited light resources adjusts its structure and growth rate to the available radiation. Perfect adjustment, however, is impossible because environments change. He indicated that plant canopies are usually compromises and balances between respiratory costs and photosynthetic advantages.

Daylength affects plants through phenological responses (flowering, etc.); therefore, it is difficult to determine the exact effect of daylength on other factors (Evans et al. 1964). McCloud and Bula (1973) suggested that knowledge of the photoperiod responses of the various forage species would facilitate development of management systems that are best adapted to different climatic regions.

Atmosphere

The atmosphere contains gases required for photosynthesis (CO_2) and respiration (O_2) and is a source of nitrogen. Larcher (1980) stated that environmental factors affect dry matter production by way of their effects on CO_2 exchange and the carbon balance. Production was greater with increased radiation from either higher intensity or longer exposure. Dry matter production, like photosynthesis, exhibited a temperature optimum, and both water deficiency and inadequate or unbalanced provision of nutrients reduced the production of matter. Complete agreement, however, between variations in production rate and gas exchange is not always expected since environmental factors affect not only the uptake of carbon but also transport of assimilates and hormonally controlled activities in the plant. All of these processes may be affected in the same direction but to different extents, thereby causing discrepancies.

Pollutants or toxic substances also occur in the atmosphere. They are released into the environment by activities such as industry, traffic, agricultural and domestic use of chemicals, and consumption of fossil fuels. Plants may absorb these substances from the air, water, or soil (Larcher 1980). He indicated that the atmosphere pollutants which are particularly dangerous to plants include sulfur dioxide (SO_2), hydrogen halides (HF, HCl), ozone, and peroxi-acetyl- nitrate (PAN, produced from automotive and industrial fumes under strong radiation). Other harmful substances in the air include nitrogen oxide (NOx), ammonia (NH_3), hydrocarbons, tar fumes, soot, and dust. Larcher (1980) compiled a list giving sensitivity of agricultural, ornamental, and forest plants to chronic exposure to SO_2, HF, HCl, and NOx from a general survey. He emphasized that plant sensitivity could be quite different among species of the same family and even among individual ecotypes or varieties.

Research conducted in the mixed prairie of Montana (Dodd et al. 1982) showed no short-term effects on plant biomass dynamics, aboveground net primary production, or total belowground biomass dynamics under low levels of SO_2. However, short term reduction in rhizome biomass of western wheatgrass (*Agropyron smithii*) occurred, and the biomass of Japanese brome (*Bromus japonicus*) was reduced during one season. In other studies reported by Lauenroth et al. (1985) senescence of western wheat grass leaves were altered by SO_2, but standing crop and above ground net primary production remain unaffected. Data presented by Lauenroth et al. (1985), however, suggested that the effect of SO_2 exposure on regrowth following defoliation can alter end-of-season standing crop.

Wind, another component of the atmosphere, can affect plant productivity. The main influences of wind are increased evapotranspiration, physical damage to plants, and mixing of gases, particularly within canopies.

Nutrients

Vallentine (1980) and others reported that nutrient deficiencies in the soil resulted in reduced forage production, modified vegetation composition, and altered nutrient content of the forage. Nitrogen has been reported to be a major nutrient limiting plant growth in several regions (Owensby et al. 1970; Wight 1976; James and Jurinak 1978; Morrow et al. 1978; Fischer et al. 1987). Nitrogen fertilizer has increased vigor of grasses, particularly cool-season grasses, through increased basal area per plant, height and number of seed stalks per plant, seed production, size of stems and leaves, and number of roots (Vallentine 1980). Wight (1976) reported that nitrogen fertilizer has also increased water use efficiency and improved forage quality and palatability. Growth responses to nitrogen fertilizer can be large but vary with availability of soil moisture (Sneva and Hyder 1965; Wight and Black 1979; Power 1983; Rauzi and Fairbourn 1983).

Phosphorus generally does not significantly affect yield of grassland herbage or plant vigor unless phosphorus levels in the soil are quite low or phosphorus is applied along with high rates of nitrogen (Vallentine 1980). Growth of legumes, however, has been stimulated by phosphorous fertilizer. Sneva (1986) suggested that sulfur deficiencies may occur in crested wheatgrass (*Agropyron desertorum*) stands being fertilized with nitrogen.

Shifts in species composition have been reported on mixed prairie following fertilizer applications in North Dakota (Rogler and Lorenz 1957, Lodge 1959, Goetz 1969, Lorenz and Rogler 1972, Goetz et al. 1978). Generally the stand has changed from one dominated by a short warm-season grass, blue grama (*Bouteloua gracilis*), to one dominated by a cool-season midgrass, western wheatgrass. Shifts have also occurred in the sagebrush-bunchgrass steppe of eastern Oregon (Sneva 1963) and central Washington (Patterson and Youngman 1960) where cheatgrass (*Bromus tectorum*) has increased at the expense of native bunchgrasses.

In general, most cool-season grasses respond favorably to nitrogen fertilizer while some warm-season grasses do not. The differential response has been attributed to differences in season of growth. Cool-season grasses grow mostly in early spring when moisture is less limiting and when the release of soil nitrogen is slower (Vallentine 1980).

Recent work on rangelands has focused on evaluating the symbiotic relationship between vesicular-arbuscular mycorrhizae fungi and plants. Emphasis has been on taxonomy, rate of infection (particularly on mine spoils), plant establishment, growth of infected plants, and response of mycorrhizae to soil compaction and grazing of infected plants. Trappe (1981) reported that mycorrhizal fungi grew between or into cortical cells of hosts rootlets and out into the surrounding soil. Nutrients absorbed by the fungus from the soil were translocated to the hosts, and photosynthates and their derivatives were extracted from host tissues by the fungus. In essence, the fungal hyphae extended into the soil and served as an extension of the root system.

Several studies have shown that vesicular-arbuscular mycorrhizae fungi improved plant absorption of phosphorus, nitrogen, and other elements (Mosse 1973, Gerdemann 1975, Clarkson and Hanson 1980, Bowen and Smith 1981) and increased growth of plants (Gerdemann 1975, Aldon 1978, Green et al. 1983, Call and McKell 1984). Bethlenfalvay and Dakessian (1984) reported that density of forage grasses and their colonization by vesicular-arbuscular mycorrhizae fungi was significantly reduced as a result of grazing. The decrease in fungal colonization was ascribed to a decrease in leaf areas and an increase in root to shoot ratio-conditions which resulted in decreased source capacity and increased sink demand. Mycorrhizal colonization of little bluestem (*Schizachyrium scoparium*) roots was reduced by soil compaction but was increased by clipping (Wallace 1987). Wallace emphasized that further work is needed to understand the combined influence of clipping and soil compaction on plant and mycorrhizal growth and development as well as on their recovery from these stresses.

Fire

Fire can affect plants directly through heat damage to individuals or indirectly by reducing competition and releasing resources (water, nutrients, light). Scifres (1980) reported that plant responses to fire vary with plant morphology and phenological stages of development. Young (1983) reported that trees and shrubs and some perennial forbs have growing points elevated on aerial stems, and these are often severely damaged by fire. He indicated that survival of these species is dependent upon the ability to resprout after aerial stems are lost. In contrast, most grasses and forbs have growing points insulated from heat injury since they are located near or below the soil surface. Young (1983) indicated that the degree of damage sustained by these species is proportional to the temperature and length of time meristematic tissues are exposed to elevated temperatures. Generally, there is an increase in flowering and herbage production during the first year after burning grasslands, but the response varies with precipitation and season of burning (Risser 1985). This increased productivity has been reported in most grassland types, ranging from the tallgrass prairie to mountain grasslands. Generalized response of individual plant species to burning has been reported in the literature (Wright et al. 1979; Vallentine 1980; Wright and Bailey 1980, 1982; Young 1983).

Grazers

A portion of the leaf and shoot tissue is removed when plants are grazed by livestock, wildlife, or insects. Hyder (1972) stated that if all other elements are equal, plant growth is a function of the amount of leaf tissue exposed to sunlight. Caldwell et al. (1981) also showed that culms and leaf sheaths of grasses were important for carbon uptake during certain periods of the growing season. With defoliation, Risser (1985) reported that a number of predictable responses occurred in grasses. Some plants re-

sponded by increasing the assimilates allocated to young leaves or regrowing tillers. In others, an increase in root mortality and a decrease in root extension and branching occurred when shoots were clipped too frequently or severely. The damaging impact of high frequency and intensity of defoliation which occurs at certain seasons and phenological stages of development has been reported by many authors (Biswell and Weaver 1933; Daubenmire 1940; McIlvanie 1942; Stoddart 1946; Blaisdell and Pehanec 1949; Crider 1955; Oswalt et al. 1959; Dyer et al. 1963; Jameson 1963, 1964; Davidson and Milthorpe 1966a, b; Wilson et al. 1966; Harris 1967; Trlica and Cook 1971; Drawe et al. 1972; Dyer and Bokhari 1976; Harris and Gobel 1976; Buwai and Trlica 1977; Hodgkinson and Baas-Becking 1977; Detling et al. 1979; Miller and Donart 1981; Westoby 1980; Mutz and Drawe 1983; Mclean and Wikeem 1985a, b; McShane and Sauer 1985; Eckert and Spencer 1987).

Moderate defoliation, however, can stimulate above ground production in some species (Gay and Dyer 1965, Hyder 1972, McNaughton 1979, Cable 1982, Heitschmidt et al. 1982, Provenza et al. 1983, Lewin 1987). Lauenroth et al. (1985) suggested that such compensatory growth following grazing in grasslands may result from a number of indirect effects on microclimate. Examples include: (1) increasing light penetration to lower canopy leaves and (2) prolonging the period of favorable soil moisture by reducing evapotranspiration. In addition, some individual plants respond to defoliation by increasing photosynthetic rates in remaining or newly developing leaves (Lauenroth et al. 1985). Either strategy increased the proportion of current photosynthate allocated to the synthesis of new leaves.

In addition to conventional grazers, soil inhabiting nematodes also feed on plants. Smolik (1977) applied a nematicide to heavily-grazed range in western South Dakota and found increases of aboveground harvestable herbage ranging from 28-59% with decreases of plant feeding nematodes ranging from 87-96%.

Hyder (1972) reported that resistance to grazing improved with an increase in leaf replacement potential, which varies with stage of growth as well as among species. He cautioned that over-emphasis of resistance to grazing is unwise because this characteristic is inversely related to herbage productivity. After defoliation, regrowth could arise from existing active meristematic tissue (usually fast) or from previously quiescent axillary buds (usually slow). Consequently leaf replacement was most favorable from culmless vegetative shoots, intermediate from culmed vegetative shoots clipped above the apical meristem, and least from reproductive shoots clipped above or through the rudimentary inflorescence. For the latter two cases, where clipping of leaves resulted in leafless culms, the most favorable leaf replacement can be attained by scheduling the time and height of defoliation in order to stop culm growth and promote new tillers. Hyder suggested that machine harvest or rotational grazing is indicated for culmed shoots, but continuous grazing is more appropriate for grasses with culmless vegetative shoots. Dahl and Hyder (1977) indicated that shrubs like fourwing saltbush and bitterbrush are vulnerable to yield reduction by excessive grazing. One must adjust grazing for such shrubs to retain most of the apical meristems throughout the growing season or during active periods of growth. This can be accomplished by providing periods of non-use or only light grazing.

Miller (1986) summarized the responses of cool-season grasses to defoliation. Responses to moderate defoliation varied with the phenological stage at which treatment occurred. In the vegetative phase, defoliation provided for maximum regrowth and had a minimum effect on plant vigor and on current year's production. During the flowering phase, defoliation: (1) induced tillering when sufficient soil moisture was available, (2) reduced current year's total forage crop, and (3) stimulated maximum leaf production and reduced plant vigor. At maturity, defoliation had little effect on the current year's production and little to no effect on plant vigor.

The removal of foliage from a plant reduces to some degree its potential to compete and retain its status in the community (Caldwell 1985b). Caldwell also indicated that competitive pressure may determine tolerance of herbivory. In this regard, Mueggler (1972) found that the extreme effect of defoliation on bluebunch wheatgrass (*Agropyron spicatum*) during a sensitive period could be partially offset by reducing competition from adjacent plants. Caldwell (1985b) suggested that the reduction in leaf area and root system activity that occurs with defoliation may delay or reduce the capacity of the plant to utilize water and nutrients during the short period of time of availability in semiarid environments. This delay in use can mean forfeiture of use when there is competition.

Grazers, as well as man, affect watershed hydrologic properties of rangelands by removing protective plant cover and by trampling (Blackburn et al. 1982). They reported that through reduction in vegetative cover, the impact of raindrops may increase; soil organic matter and soil aggregates may decrease; surface crusting may increase; and infiltration rates may decrease. They suggested that resulting consequences may include increased overland flow, reduced soil water content, and increased erosion. These changes could, in time, affect plant productivity on these rangelands.

Competition

Plants grow in communities where they compete with neighbors for resources (Rhodes 1970, Harper 1977, Miller et al. 1980, Allen 1982, Christie and Detling 1982, Fowler 1986). Therefore, ever changing environmental conditions may provide enhanced growing conditions for one plant species over another. This phenomena influences some of the shifts in plant species occurring with fertilization of native range, periodic drought, severe defoliation, and flooding.

Modeling

Plants are constantly being affected by a combination of environmental factors. This phenomena has been known for a long time, and attempts have been made world wide to analyze the relationships and develop regression equations and models to predict plant productivity (Smoliak 1956; Sneva and Hyder 1962; Currie and

Peterson 1966; Sneva 1977; Sims and Singh 1978a, b; Grace et al.1981; Stout et al. 1981; Thomas and Norris 1981; Wight and Hanks 1981; Kindschy 1982; Quinton et al. 1982; Hanson et al. 1983; Sneva and Britton 1983; Wight et al. 1984; Zelawski and Szlenk 1984; Norris 1985; Stout and Brooke 1985; White 1985; Brown et al. 1986; Holt and Haferkamp 1987). These activities are continuing today, and some of the more recent efforts are presented in this proceedings.

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