ASSESSING PHYSIOLOGICAL REQUIREMENTS OF PLANT SPECIES AS A PREREQUISITE FOR THEIR USE IN MINE RECLAMATION[1]

by

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Abstract. Plant growth occurs when resource availability is sufficient to meet the plant's physiological requirements. Plants have four major resource requirements: energy, water, carbon, and nutrients. A shortage as well as an over-abundance of just one of these resources can disrupt plant physiological processes, with a concomitant reduction in plant growth or survival. The plant kingdom as a whole has a large range in physiological requirements, and even the physiological requirements of different species from the same plant community can differ. Although many options are available for plants to acquire and allocate the resources needed to meet their specific physiological requirements, any individual plant can only utilize a limited number of these options. Furthermore, each selected option has different benefits and costs. Thus, the success of reclamation projects can be greatly enhanced by carefully considering which physiological strategy may match the environmental constraints of the area, then choosing for revegetation those species that have these options.

Additional Key Words: Plant growth; energy balance; water balance; carbon balance; nutrient balance.

Introduction

Plant growth occurs when the availability of resources meets or exceeds the plant's requirements for physiological functioning. The plant kingdom as a whole has wide amplitudes of both physiological requirements and stress tolerance mechanisms (Fitter and Hay 1987), but a particular plant species has only limited tolerance ranges for any one environmental factor. Knowledge of this suite of tolerance ranges is critical for successful reclamation. For example, species for reclamation in the semiarid Great Basin need to tolerate hot dry summers, whereas species for reclamation in montane forests may need to contend with long periods of suboptimal temperatures rather than hot or dry climatic conditions. Soil conditions such as texture, salinity, and pH affect water and nutrient availability, with concomitant effects on plant growth. Biotic interactions, which include plant-plant, plant-animal, and plant-microbe interactions, need to be considered. Finally, the major uses of the land after reclamation, whether for grazing, recreation, aesthetics, or wildlife habitat, must be carefully defined because of their different physiological requirements.

This paper presents a framework to determine which physiological characteristics are appropriate for a specific reclamation project. The paper is organized around the four major resource requirements of plants (Larcher 1980): energy, water, carbon, and nutrients. For each resource, three major considerations are examined: 1) what are the options that are available to plants to gain a particular resource; 2) what must plants do with

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these resources in order to survive; and 3) how much discretion do plants have to allocate their resources. Although I primarily cover general concepts, I also consider applications to specific problems for reclamation in arid and semiarid lands.

Energy Balance of Plants

The temperature of plants is determined by the difference between heat gain and heat loss, i.e. net energy balance. Seven components must be considered (Campbell 1977; Gates 1980): metabolic heat; solar or shortwave radiation; terrestrial or longwave radiation; convection; conduction; evapotranspiration (ET); and storage.

Two of these components generally play very small roles in the energy balance of plants. With very few exceptions, the amount of metabolic heat generated by plants during respiration and other metabolic activities is very small and can be ignored. Over long periods of time, net storage is also negligible: energy stored is eventually lost. However, for a few species with fleshy leaves or stems, storage can provide a temporary source or sink of heat to survive short periods of unfavorably cold or hot weather conditions. Some of the best known examples are the large cacti in the southwestern desert of North America (Nobel 1985).

Shortwave radiation is exclusively an energy gain. Only a small portion of solar energy (1-2%) is used to drive photosynthesis (Nobel 1991). The remainder of the solar energy is absorbed or reflected by plants. Plants can alter shortwave radiation absorptance by modifying leaf and stem optical properties, such as by increasing pubescence, and through changes in leaf or stem orientation (Ehleringer 1985).

Plants gain and lose energy through longwave radiation. All objects in a particular plant's "field of view" emit radiation that impinges on the plant, and in turn the plant radiates longwave radiation to these same components of its environment. Thus, where a plant is located, such as under the canopy of another plant, under the shade of a rock, or in the open, affects its net longwave radiation exchange. During the daytime, heat gain from longwave radiation generally accounts for about 50% of total energy gain, but this gain is more than balanced by heat loss through longwave

radiation emission (Nobel 1991). At night, especially for a plant in the open under a clear sky, longwave radiation can account for 75-90% of the plant's heat loss, and thus leaf temperature can drop several degrees below air temperature.

Convection can be either a heat loss or heat gain, depending on if plant temperature is greater than or less than air temperature. Both plant and environmental factors affect convective heat exchange. Leaf size and shape as well as height above the ground are plant factors, and wind speed is the most important environmental factor (Nobel 1991). In general, small leaves, especially those in windy conditions, tend to be close to air temperature. Large leaves or leaves in very calm microenvironments can deviate 5-10 °C from air temperature (Gates 1980).

Conduction is generally not important for aboveground portions of plants, but is the only process of heat exchange for root systems. Almost without exception, root temperatures are the same as the temperature of the surrounding soil. Although root physiological processes such as nutrient uptake are affected by temperature, plants have very little control over short-term changes in root temperature.

ET is the only component of energy exchange that plants can change reversibly and in the short-term (seconds to minutes) to modify its energy balance. The other options, such as changes in leaf optical properties or leaf size, are long-term and relatively fixed modifications. Changes in transpiration rates are easy and metabolically cheap, as long as water is available.

Plants used for reclamation purposes are exposed to freezing as well as high temperatures. Mechanisms for freezing resistance include:
1) Avoidance (dormancy, thermal mass, insulation, prevent ice formation)
2) Tolerance (tolerate ice formation within cells)
Mechanisms for high temperature resistance are analogous:
1) Avoidance (dormancy, modify energy exchange)
2) Tolerance (prevent protein denaturation, maintain cell membrane integrity)

Water Balance

Water is vitally important for many plant processes: biochemical reactions, transport of

nutrients and food, structure of plants, plant growth. Water is often the primary limiting factor for vegetation in arid and semiarid lands (Smith and Nowak 1990), and even reclamation in mesic climates can be hindered by soil-induced drought conditions.

Water stress develops when the rate of water uptake exceeds the rate of water loss. Water stress occurs on both diurnal and seasonal cycles, especially in arid climates. On hot, dry days, many plants experience severe water stress during midday, even though soils may be relatively wet. Because of the high evaporation gradient from a saturated leaf to a dry atmosphere, plants have high transpiration rates that exceed the abilities of the root system to take up water from the soil and/or of the vascular system to supply water from roots to leaves. Seasonal patterns of soil water depletion are the primary cause of seasonal patterns of plant water stress.

Different groups of plants have different ranges of tolerance to water stress and can tolerate different minimum values of plant water potential (Larcher 1980). In general, plants have three basic mechanisms to cope with water stress:

1) **Drought escape** occurs when vegetative tissues are never exposed to drought stress. Good examples are ephemeral plants such as desert annuals which set seeds and senesce before drought conditions develop. These plants "escape" drought by persisting through drought periods as seeds. The germination requirements for many of these species are very complex and are affected by temperature, soil water status, etc. (Ehleringer 1985). These species generally comprise only a small proportion of mine reclamation projects because they do not provide predictable and perennial plant cover.

2) **Drought postponement** is probably the most prevalent mechanisms among plants. For this mechanism, plants adjust their physiological, anatomical, or morphological attributes in order to increase the availability of water; i.e. plants postpone the initiation of severe water stress by changes that increase the effective water supply to living tissues. Four of the most common methods to postpone drought include:
a) water storage. Cacti are excellent examples of plants that maintain specialized water storage tissues which have adequate water reserves to maintain an individual plant for months or, in some cases, for years. The woody stems of large trees and shrubs also store sufficient water for short time periods from hours to days. However, the residence time of water in most plant leaves is very short, on the order of minutes to hours (Nobel 1991).
b) improve water uptake. Particular rooting patterns, such as fine and highly branched root systems or very deep roots that tap shallow groundwater (known as phreatophytic plants), increase the amount of soil water that is available to plants. Some plants, especially some of the desert cacti, rapidly initiate root growth in response to rainfall. In the Great Basin, many species have patterns of root growth that precede a "wetting front" within the soil profile (Caldwell 1985).
c) restrict transpiration. If a plant is able to reduce transpiration, then soil water is conserved for future use. In general, plants have three methods to reduce transpiration. First, they can reduce the amount of transpiring leaf area. For example, plants with drought deciduous leaves (i.e. leaves that are lost when drought stress starts) such as sagebrush in the Great Basin and palo verde in the Sonoran Desert are good examples. A second method is to reduce heat gain, such as leaf movements, pubescence, and other methods discussed earlier. A third method is stomatal sensitivity to atmospheric and soil drought conditions. For example, increasing stomatal closure with increasing evaporation gradients reduces transpiration during midday periods of water stress, and increasing stomatal closure with seasonal increases in water stress also helps conserve water (Nowak et al. 1988). For reclamation projects in arid environments, particular attention should be given to species that have high stomatal sensitivity to atmospheric and soil drought.
d) osmotic adjustment. In order for a plant to extract water from the soil, the plant's water potential must be less than that of the soil (i.e. it must be more negative). An effective method to make the water potential of the

plant more negative is to increase the solutes within the plant cells. However, many solutes have detrimental affects on proteins, enzymes, and other cell structures. Although this method is limited to only certain organic and inorganic solutes, osmotic adjustment occurs in many plant species. As with stomatal sensitivity, plants that exhibit high capability for osmotic adjustment, especially at the seedling stage, will generally be more successful for aridland reclamation.

3) True **drought tolerance** occurs when vegetative tissues tolerate severe dehydration. Generally, mature plants are <u>not</u> drought tolerant, but often some parts of the plant (*e.g.* rhizomes, tubers, bulbs, crowns, woody tissue) are drought tolerant. The mechanisms for true drought tolerance are at the cellular level and include modifications of membranes, the cytoplasm, and proteins. As recently as five years ago, much of what was known about these molecular and cellular processes was not directly applicable for mine reclamation. However, recent advances in molecular biology will likely provide many benefits for reclamation. For example, Adair *et al.* (1992) have characterized genes in fourwing saltbush (*Atriplex canescens* (Pursh.) Nutt.) whose expression is induced by drought stress. This characterization provides two benefits: 1) a rapid technique to screen and identify clones or varieties of plants with exceptionally high drought tolerance; and 2) the ability to artificially transfer these genes to other plants to increase their drought tolerance.

Carbon Balance

Plants have three photosynthetic pathways to fix carbon: C_3, C_4, and CAM. C_3, or cool season, plants are the most common. C_4, or warm season, plants theoretically have higher water use efficiencies, tolerate higher temperatures, and have potentially greater photosynthetic rates than C_3 plants, but C_3 plants are generally "superior" to C_4 plants at lower temperatures. CAM, or succulent, plants are the most water use efficient, but generally have the lowest photosynthetic and growth rates.

Although the C_4 and CAM photosynthetic pathways are thought to be superior in arid climates, C_4 and CAM plants do not always dominate the landscape. For example, the semiarid Great Basin has very few C_4 plants (Smith and Nowak 1990). Even one of the most common C_4 plants, *Atriplex confertifolia* (Torr. & Frem.) Wats. (shadscale), has photosynthetic characteristics that are very similar to that of the C_3 plant *Ceratoides lanata* (Pursh.) J.T. Howell (winterfat) (Caldwell 1985). The lack of significant summer rainfall is the likely reason for the low proportion of C_4 species in the Great Basin (Smith and Nowak 1990). In hot deserts with both winter and summer rainfall, C_3 plants generally are activated by winter rains whereas C_4 plants are activated by summer rains.

Carbon gain through all photosynthetic pathways is influenced by light, temperature, and other environmental factors (Gates 1980; Fitter and Hay 1987). Furthermore, for plants to gain carbon, they must lose water: CO_2 for photosynthesis enters leaves through stomates and follows the same pathway as water loss. Thus, photosynthesis is also indirectly affected by transpiration: when plants close stomates to reduce transpiration, they also reduce photosynthetic rates. Recent techniques have allowed us to relate patterns of water use efficiency, *i.e.* the ratio between carbon gain and water loss, to patterns of plant distribution and responses to environmental conditions (Ehleringer 1988). For example, water use efficiency for three Great Basin species, *Ceratoides lanata*, *Elymus lanceolatus* (Scribn. & J.G. Smith) Gould (thickspike wheatgrass), and *Elymus elymoides* (Raf.) Swezey (squirreltail), increased with nitrogen fertilization, but decreased with irrigation (Toft *et al.* 1989). However, water use efficiency of *Artemisia tridentata* Nutt. ssp. *wyomingensis* (sagebrush) was affected by irrigation, but not by fertilization. These results can be applied to mine reclamation: if a particular project is likely to encounter drought conditions, then application of nitrogen fertilizers may help certain plants persist through the drought period because of increased water use efficiency.

Plants allocate the carbon that is fixed by photosynthesis to maintenance, growth, and/or storage. Maintenance costs for plants are affected by the amount of biomass that is degradable (proteins, enzymes, membranes, stored carbohydrates, etc.) as well as how fast these

compounds degrade (Ryan 1991). Degradation rates are influenced by temperature and plant growth stage. After maintenance costs are met, plants can allocate the remaining carbon to either growth or storage. Growth costs are proportional to the growth rate of structural and nonstructural biomass that needs to be synthesized. The conversion efficiency of photosynthetic end products into structural and non-structural biomass is 70-75% for most plants and is affected by biosynthetic costs as well as non-synthetic costs such as translocation, RNA transcription, enzyme production, etc. Costs to produce storage compounds are similar to growth costs.

Nutrient Balance

Nine elements are considered essential macronutrients: carbon (C), hydrogen (H), oxygen (O), nitrogen (N), phosphorous (P), sulfur (S), calcium (Ca), magnesium (Mg), and potassium (K) (Marschner 1986). These elements are essential for plant metabolic and growth processes and comprise the bulk of plant tissues. C, H, and O are 85% or more of a plant's dry weight. N, Ca, and K contribute another 12%, and P, S, and Mg total approximately 2% of plant dry weight.

The remaining 1% of a plant's dry weight comes from 20-25 other elements that are commonly found in plants. Sodium (Na) and chlorine (Cl) are the two most abundant essential micronutrients, but generally each comprises less than 0.1% on a dry weight basis. Iron (Fe), manganese (Mn), zinc (Zn), and boron (B) are essential micronutrients that have dry weight concentrations of less than 300 ppm. Copper (Cu), molybdenum (Mo), cobalt (Co), vanadium (V), gallium (Ga), silicon (Si), and iodine (I) are micronutrients that are present in trace amounts. Other elements such as aluminum (Al), selenium (Se), strontium (Sr), rubidium (Rb), chromium (Cr), tin (Sn), nickel (Ni), fluorine (F) and bromine (Br) do not appear to be essential for plant growth, but can be present in trace amounts. Some of these latter elements can partially substitute for other essential nutrients, such as Sr for Ca or Rb for K, but plants can grow without them.

If one or more of these nutrients is present in relatively low or high concentrations, plant growth is adversely affected. Reduced growth rates, stunted plants, and yellow, chlorotic leaves are typical symptoms of nutrient deficiencies. If the trace elements Al and Se are present in excessive concentrations, they are often toxic to plants. Even excess essential nutrients such as Ca, K, or Mg can have detrimental effects. For the reclamation of mined lands, species that accumulate large quantities of metals with little or no toxic effects are especially interesting for certain applications (Hewitt and Smith 1975). For examples, *Atriplex canescens* and a number of *Astragalus* species accumulate selenium, *Sarcobatus* species (greasewood) accumulate uranium, and *Pseudotsuga menziesii* (Mirb.) Franco (Douglas fir) accumulates arsenic.

Physiological and morphological characteristics of plants influence ion uptake from the soil (Fitter and Hay 1987; Marschner 1986). Plant roots have specialized enzyme systems to selectively uptake or exclude certain elements, but these systems require aerobic conditions and a supply of carbohydrates. These enzymatic systems influence the rate of ion uptake as well as the ability to extract ions when they are present in low concentrations. A large demand for an ion, such as a demand queued by low cellular concentrations due to fast growth rates, can also increase uptake rates. Morphological characteristics of root systems also influence the ability to take up nutrients. For example, under nutrient deficient conditions, plants often allocate relatively more resources to roots than shoots, resulting in higher root:shoot ratios (Fitter and Hay 1987). Root diameter and root hairs may enhance nutrient uptake for immobile ions, but probably play relatively minor roles for other nutrients. Root age influences uptake of some ions such as Ca, but other nutrients such as P and K are not greatly affected. Root density and distribution may be the most important characteristic for nutrient uptake when nutrients are limited or immobile (Caldwell and Richards 1986).

Plants have also developed specialized biotic interactions to cope with low nutrient availability (Fitter and Hay 1987). The mycorrhizal symbiotic relationship between plant roots and fungi enhances nutrient uptake, especially for relatively immobile ions like P. Nitrogen fixation by symbionts such as legumes and bacteria can be an important source of N for the host plant as well as neighboring, non-infected species. Two other mechanisms, parasitism and carnivory, exist, but

are generally rare.

The predominant strategy among wildland plants to tolerate infertile soils appears to be inherently slow growth rates coupled with large root systems (Chapin 1980). Some species exhibit "luxury consumption", *i.e.* uptake and accumulation of more nutrient than is needed for growth and metabolism, but few plants store large quantities of nutrients for long periods of time. In addition, plants "recycle" nutrients: they retranslocate macronutrients such as N, P, K, and Mg from senescing tissues to growing tissues. Although recycling nutrients benefits plants that grow on infertile soils, this characteristic is found in many plant species from a wide variety of habitats.

Summary

By carefully selecting species whose physiological requirements match the environment that will be experienced during reclamation, the success of that reclamation project can be enhanced. The reclamation specialist should first consider the extent that each plant resource may be in limiting supply and, in some cases, in overabundance. Only after determining what resource is the most limiting can plants with the appropriate mechanism(s) to tolerate that stress be selected. Unfortunately, the specific mechanisms that a particular species employs to overcome environmental stress are generally not well known for many wildland species. None-the-less, we can often infer the mechanisms from the morphological and phenological characteristics of the species. Even without a complete understanding of the mechanisms that plants employ, knowledge of what resources limited plants under natural conditions or in an earlier, successful reclamation project can be used to guide the selection of species for a reclamation project with similar limiting resources.

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