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Predicting Invasive Species Impacts on Hydrological Processes: The Consequences of Plant Physiology for Landscape Processes¹

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Abstract: The adverse impacts of invading alien organisms are widely recognized as one of the major threats to biodiversity and are receiving growing recognition as a major socioeconomic threat. The hydrological impacts of alien plants have received less attention, despite growing evidence of their significance. The wide range in plant growth forms and physiology among invading species suggests that estimation of the hydrological impacts could be difficult. The concept of limits to evaporation was developed to help organize our general scientific understanding of the hydrological implications of changes in vegetation. It provides a way of reducing this complexity to the factors most likely to be the major determinants of evaporation from vegetation in a given situation. It distinguishes between physical factors (1) availability of energy from solar radiation and advection, (2) availability of soil moisture at landscape and habitat scales, and (3) raindrop size, and biological factors (4) plant size, including height and rooting depth, and (5) plant physiology, including seasonality of the leaves and drought tolerance. Studies of the hydrological impacts of vegetation change invasion show that changes in vegetation structure and seasonality can have significant impacts on water resources at both habitat and landscape scales. Invasions can also have significant impacts where the invaded habitat has more water available within the rooting depth than adjacent areas.

INTRODUCTION

The adverse ecological and economic impacts of invading alien organisms are widely recognized (Pimentel 2001; Vitousek et al. 1996). Many countries have established programs to limit new introductions and to deal with the impacts of existing invaders—notably Australia, New Zealand, and some states in the United States—and the Global Invasive Species Program is developing international guidelines (Mooney et al. 2004). South Africa appears to be unique because the primary motivation for the national Working for Water Program is the adverse impact on water resources (Calder and Dye 2000; Le Maitre et al. 2000; Van Wilgen et al. 1997) rather than impacts on biodiversity.

One of the problems in understanding the hydrological impacts of invading plants is that they comprise a number of life forms (ranging from herbs and grasses to trees), have widely varying physiological traits (evergreen or deciduous, succulents to phreatophytes), and often occur in mixtures. The natural plant communities

that they replace also vary widely and comprise mixtures of species. Although the number of studies of hydrological impacts of invaders is limited, there is a large body of relevant information available from studies of the impacts of changes in vegetation on hydrology, at scales ranging from large catchments to plant communities and individual plants (Bosch and Hewlett 1982; Jarvis and McNaughton 1986). These studies have shown that there are a number of general relationships that can provide insights into the kinds of impacts that could be caused by different kinds of invaders invading different kinds of vegetation.

THE LIMITS CONCEPT

Evaporation from vegetation is generally the second largest component of water balance (after rainfall) and the most difficult to measure (Calder 1999). There are many techniques and models for estimating evaporation (Et) from vegetation, where Et = transpiration plus interception losses. Most of them are based on estimating the amount of energy available to drive Et from climatic data and reducing this "potential Et" to allow for various factors that reduce evaporation in practice to "actual Et" (Jarvis and McNaughton 1986). Most of these ap-

¹ Received for publication January 29, 2004, and in revised form June 2, 2004.

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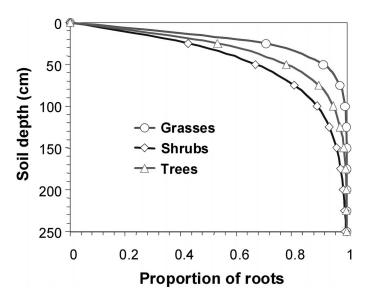


Figure 1. Root depth distributions for plants with different growth forms based on data compiled by Jackson et al. (1996).

proaches do not explicitly include vegetation factors as potential controls on evaporation, use hypothetical vegetation, or use parameters that are technically demanding to measure. The limits concept developed by Calder (1996, 1999) proposes that there are four kinds of factors which limit Et, with no more than two being important in any given situation. The limiting factors can be grouped as physical factors, namely (1) energy availability from solar radiation or, in certain situations, advected energy;³ (2) soil moisture availability, especially in strongly seasonal climates; (3) precipitation droplet size and its effect on interception; and biological factors, namely (4) plant physiology, for example, whether vegetation is evergreen or deciduous or its moisture stress tolerance; and (5) plant size (height, stem diameter, leaf area) and depth of the root system. In arid and semiarid environments, the primary limiting factor in dryland situations will be moisture availability, and in subarctic or humid tropical regions, evaporation generally will be limited by energy availability. Between these extremes and in environments such as riverine alluvial deposits where additional moisture is available from groundwater, the other factors will become important.

APPLYING THE CONCEPT

Two examples have been selected to illustrate the application of the limits concept at different spatial scales.

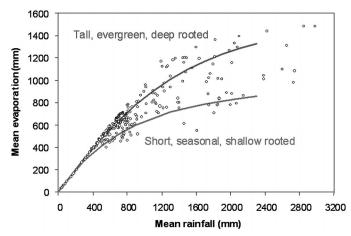


Figure 2. Relationship between mean annual rainfall and mean annual evaporation for a range of catchments worldwide, with general curves for pasture with seasonal grasslands and evergreen, deep-rooted woodlands superimposed (after Zhang et al. 1999).

At the plant or community scale, the growth form of a plant can provide an important indication of the kinds of changes that can be caused by invasions. Tall woody plants typically have deeper root systems than herbs and grass species (Jackson et al. 1996, Figure 1). This implies that where tall woody species replace grasses, they will be able to access a greater volume of the soil and extract more water than the grass species (provided that the roots systems can reach greater depths and additional moisture is available). The taller, rougher canopies of the woody species also increase evaporation losses by increasing the circulation of the air and, thus, canopy conductance (Jarvis and McNaughton 1986). When replacement of grasses by woody species occurs at the scale of a catchment, then these changes become manifest in the changes in evaporation (Figure 2). The two curves in this figure demonstrate the general trends that can be expected when evergreen woodlands are replaced by seasonal grasslands (Zhang et al. 1999), thus illustrating the combined impacts of changes in two biological factors: seasonality of the leaves in the canopy and changes in plant size and root depth. The curves also provide a firstorder estimate of the magnitude of the changes that can be expected.

A different example is provided by serial invasions, where annual grasses replaced woody vegetation and are now being replaced by a deeper rooted thistle species (Gerlach 2004). In this case, the initial invasion is likely to have resulted in an increase in surface runoff, but the subsequent invasion may decrease runoff again by as much as 25% of the rainfall.

Alluvial deposits in river floodplains can store large volumes of water after recharge during annual high flows

³ An influx of additional energy into an environment; for example, hot, dry air from a dry landscape moving into a cooler, moist riparian environment, which can increase transpiration rates.

of periodic floods. Invasions of these environments by species that can access the stored groundwater can result in high water losses. These water losses are aggravated in semiarid and arid environments because there is abundant energy from solar radiation as well as advected energy supplied by the movement of hot, dry air into the moist environment from the adjacent dryland areas. An example of this type of situation is the replacement of natural woodland by dense stands of an invasive tamarisk species. Measurements of evaporation suggest that water losses can reach 20 mm/d or 1.6 to 2.0 times the evaporation estimated from solar radiation, about 22% more than evaporation from woodlands dominated by native species (Sala et al. 1996). Across the southwestern United States, the total loss is between about 1.4 and 3.0 billion m³ of water per year (Zavaleta 2000).

CONCLUSIONS

The limits concept developed by Calder (1996, 1999) provides a way of organizing our understanding of the potential hydrological impacts of invasions. The ultimate determinants of evaporation from vegetation are the physical factors: the availability of solar and advected energy to evaporate intercepted water and drive transpiration and the availability of soil water, particularly in environments such as floodplains where additional moisture accumulates. Within the range of environments where neither water nor energy is limiting, the biological factors become the limiting factors. Invasions by species that result in a substantial change in vegetation structure (height, rooting depth) or seasonality of the leaves will result in substantial changes in the hydrology. The biological limits operate at the plant and community scales and become manifest at the landscape and larger scales as more of the landscape, or key habitats within the landscape, become invaded. The limits concept does not provide direct estimates of the actual losses, but it does identify the key factors potentially limiting evaporation and highlights those that need to be measured to get more accurate estimates of evaporation in a given situation.

ACKNOWLEDGMENTS

I thank the CSIR and the Water Research Commission for supporting these studies, and the Ecological Society of America for covering much of the cost of me attending this conference. Special thanks also to Julie Denslow for the invitation to present this paper and for organizing a very interesting session.

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