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Ecology of water relations in plants

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Key words: plant-water relations; water-deficit; waterlogging; hydrological niche.

Abstract: Water is an important resource for plant growth. Availability of water in the soil determines the niche, distribution and competitive interaction of plants in the environment.

Table of contents

1. Introduction
 - 1.1 Importance of water for plants
 - 1.2 How does water affect the ecology of plants?
 2. Water uptake and movement through plants
 3. Water stress and plants
 4. Plant Sensing and adaptation to water stress
 - 4.1 Plant sensing of soil drying
 - 4.2 Plant adaptations to water stress
 5. Distribution of plants in response to water regime
- Glossary
References
Further Reading

1. Introduction

1.1 Importance of water for plants

Water typically constitutes 80-95% of the mass of growing plant tissues and plays a crucial role for plant growth (Taiz *et al.*, 1998). Plants require water for a number of physiological processes (e.g. synthesis of carbohydrates) and for associated physical functions (e.g. keeping plants turgid).

Water accomplishes its many functions because of its unique characteristics: the polarity of the molecule H₂O (which makes it an excellent solvent), viscosity (which makes it capable of moving through plant tissues by capillary action) and thermal properties (which makes it capable of cooling plant tissues).

Plants require water, soil nutrients, carbon dioxide, oxygen and solar radiation for growth. Of these, water is most often the most limiting: influencing productivity (Taiz *et al.*, 1998) as well as the diversity of species (Rodriguez-Iturbe and Porporato, 2004) in both natural and agricultural ecosystems. This is illustrated graphically in Figure 1.

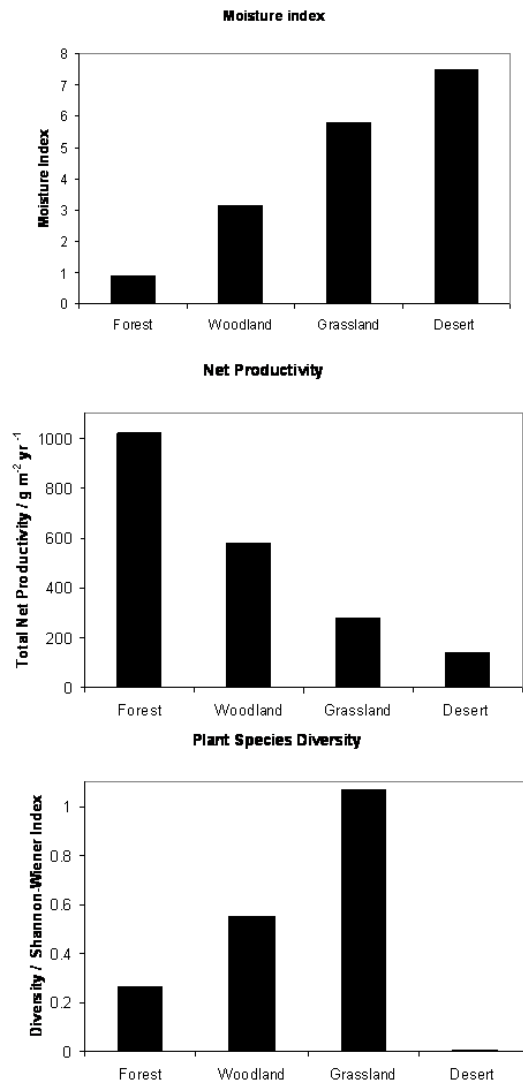


Figure 1 Moisture, total net productivity and plant species diversity of selected vegetation communities, along an elevation gradient from Santa Catalina Mountains, Arizona (after Whittaker and Niering, 1975).

The elevation gradient ranges from 1000 – 3000 metres above sea level. The Moisture Index relates to precipitation ranges of 190 mm per annum (moisture index 8) and 850 mm per annum (moisture index 1).

1.2 How does water affect ecology of plants?

In order to understand the ecology of plant water relations it is important to understand from where and how plants acquire water in their environment (the latter is discussed in Section 2).

Unlike animals, which are capable of wandering around to forage for resources, plants are for the most part stationary, depending on the availability of nutrients in their surrounding environment (soil and/or atmosphere). Of these two sources of resources, *i.e.* soil and atmosphere, the soil is by far the major and more accessible reservoir. Consequently, the soil is the primary store and regulator in the water flow of ecosystems, by intercepting precipitation input and controlling its use by organisms (Rodriguez-Iturbe, 2004). Figure 2 summarizes the soil and plant water interrelationship.

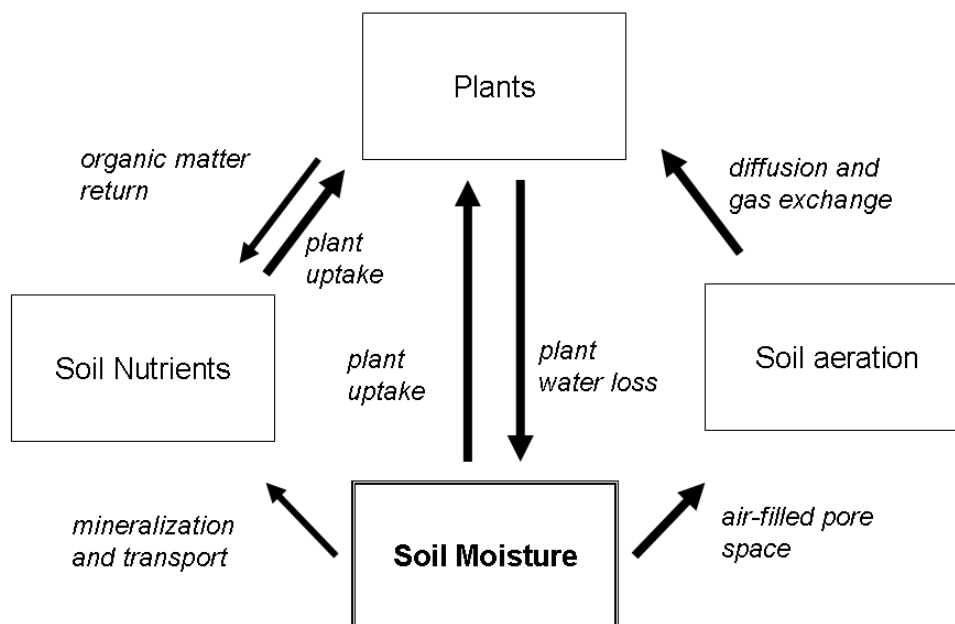


Figure 2 Schematic summary of the processes that influence the relationship between plants and soil water.

Soil moisture availability is dependent on the soil particle size distribution (also called soil texture) and arrangement of these particles (soil structure). The soil texture and structure influence the size of soil pores where water is held by capillary forces. Soils with fine-sized particles, like clay hold more water than soils dominated by coarse grain particles of sand. However, this doesn't mean all the water in fine-particle sized soils is available for plant uptake. This is because the capillary forces holding water in the pores of fine-textured soils are so powerful that the plants struggle to extract any water. Figure 3 shows soil water and soil aeration availability for different soil texture classes.

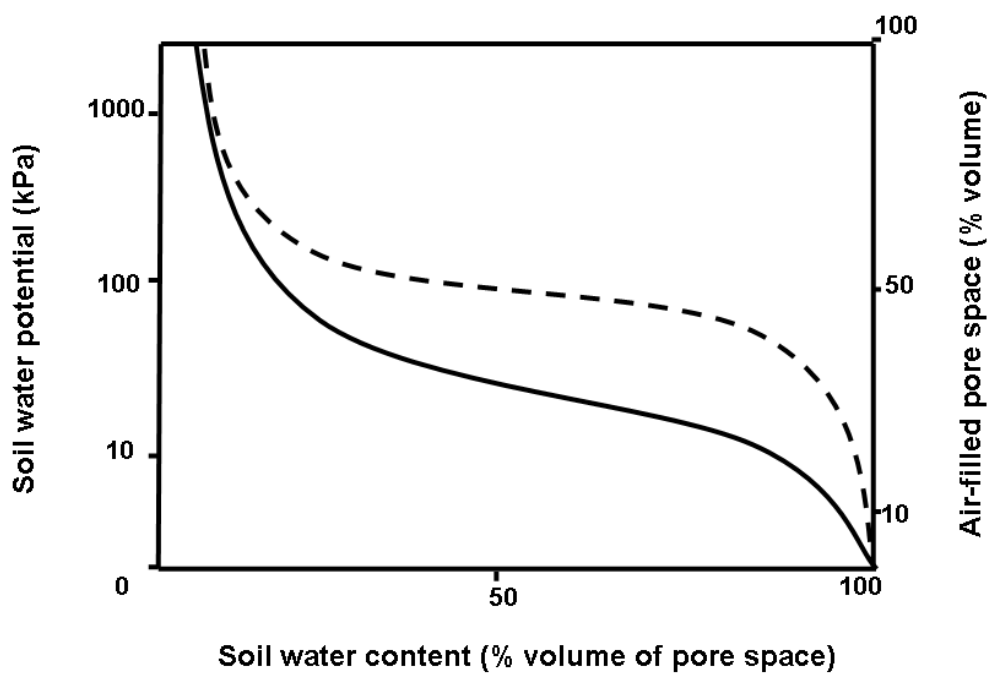


Figure 3. Soil water availability and soil aeration availability for two representative sandy (solid line) and clayey (broken line) soils. Soil water contents on volume basis is shown against soil water potential (suction) and against air-filled pore space (volume of pore space not occupied by water)

Soil moisture availability primarily influences plants by two routes (see Figure 2), either by being directly limiting as a resource, or indirectly by filling pore spaces in soil and thereby excluding air, causing oxygen availability to become limiting for the activity of plant roots. This is explained further in Section 3.

2. Water uptake and movement through plants

Water is constantly moving from the soil, into plant roots, and through the xylem tissues of the stem through to leaves where it is ultimately lost to the atmosphere during transpiration. This cycle is referred to as the soil-plant-atmosphere continuum (SPAC).

When water moves through the SPAC, it travels through different mediums (including cell wall, cell membrane and air spaces) at different distances, which utilize different modes of transport.

There are three principal modes of water transport: diffusion, mass flow and osmosis. In diffusion, water molecules move spontaneously from regions of high concentration to regions of lower concentration i.e. along a concentration gradient. This movement is rapid over a short distance and thus drives short-distance transport, for example between cells and during the loss of water to the atmosphere from leaf stomata.

In mass-flow, groups of water molecules move under an external force, such as a build-up of pressure that forms a gradient. Mass flow of water is the predominant

mode by which long-distance transport of water in stems is accomplished. It also accounts for much of the water flow through the soil and through the cell walls of plants.

The third mode, called osmosis, is movement of water molecules through a semi-permeable membrane, an example of which is the cytoplasmic membrane. Osmosis occurs spontaneously in both short-distance and long-distance transport as a response to driving forces of concentration (as in diffusion) and pressure gradient (as in mass flow).

These driving forces of water movement of both osmotic (concentration) and mass flow (pressure) origin are collectively known as water potential. Water potential is measured in units of pressure or suction i.e. force per unit area required to move a specific amount of water. The most common unit used for studying soil water potentials in the field is kilopascals (kPa).

The movement of water in the SPAC is thus dependent on differences in water potential between surrounding soil and plant or atmosphere. Often, the water potential gradient is directed from the roots towards the shoot, as transpiring leaves exposed to the atmosphere have the lowest water potential. However under situations when the soil is too dry this water potential gradient could be reversed, resulting in loss of water from plant roots to the soil. Also any environmental factors that influence the transpiration of the leaf stomata, e.g. wind or increase in temperature may further decrease the leaf water potential further, speeding up water loss.

3. Water stress and plants

In addition to an adequate level of water in their tissues, plants also require a continuous flux of water to perform vital processes such as photosynthesis and nutrient uptake. Water for these is not always available in the right quantity and quality at the right time. This imbalance in water supply and plant requirements results in plants undergoing occasional or, in some cases acute, water stress.

There are two types of water stresses that plants experience. One is when water is not available in sufficient quantity, – hence referred to as water-deficit, while the second one is that when water is available - but in excess, called waterlogging.

Water-deficit affects plants through decrease of leaf water potential, which in turn entails loss of cell turgor and stomatal closure. This results in decrease of transpiration and photosynthesis, which subsequently leads to reduced growth and if it persists, wilting. On the other hand, Waterlogging occurs when a large proportion of the pore spaces in the soil are occupied by water. This means the diffusion of oxygen and gas exchange between the soil, plants and atmosphere is limited. The result of this is decreased root growth and functioning, which negatively affects plant growth and survival.

Plants start suffering the consequences of water stress when certain thresholds for water-deficit and waterlogging are breached. Physiological plant studies have shown that soil water potentials approaching 5 kPa are sufficient to initiate plant stomatal closure, a classic response to water deficit (Henson *et al.* 1989). On the other hand,

waterlogging which cause < 10% air-filled pore space in the soil (0% is achieved at soil saturation), result in hampering root activity, and hence induce aeration stress (Wesseling & van Wijk, 1957). Between these two thresholds of drying and waterlogging stress an optimal zone conducive to plant growth is achieved (Gowing *et al.*, 2002).

However, to be even more meaningful stress thresholds need to take account of time duration, over which the plant is subjected to the stress, i.e. as short periods of stress are less damaging than gentler but longer-term ones. An index that measures this cumulates the level of stress over the time duration it occurs, and is called a Sum Exceedence Values (SEV). SEVs are calculated separately for soil drying stress and for soil aeration stress, usually in unit of metre-weeks. SEVs were originally developed in the Netherlands by Sieben and colleagues in 1960's but later on successfully used in the UK by Gowing and colleagues (e.g. Silvertown *et al.*, 1999) to integrate temporal variation in soil moisture at a scale relevant to the physiological response of plants. Moreover, SEVs take into account differences in soil type (as thresholds are specifically developed for each soil type under consideration) and are hence transferable between different sites.

4. Plant Sensing and adaptation to water stress

Water stress is damaging to plants and plants have evolved a number of short-term responses as well as life history strategies that help them cope. A mechanism that senses water stress is crucial to the initiation of defensive processes.

4.1 Plant sensing of soil drying

Water-deficit is the most common form of water stress studied in relation to sensing of impending soil drying by plant roots and the subsequent communication to shoots. In this connection, signals of a chemical nature have received a lot of attention, as they are suited for rapid communication between plant tissues.

A well-known chemical signal of impending water stress originating from exposed roots is Abscisic Acid (ABA). ABA is synthesised by dehydrating roots in non-growing tissues as well as in apices, and in the cortex (Hartung and Davies, 1991). An increase in ABA concentration in response to an increase in soil drying is known to initiate water-saving measures like reduction in transpiration rate and conductance (e.g. Henson *et al.*, 1989).

A consequence of this sensing is that it determines the response of the plant and its competitive ability. For example, a plant which responds to the tiniest sign of stress will trade-off productivity for safety (*pessimist strategy*), while a plant that waits longer will trade safety for productivity (*optimist strategy*). Depending on the extent and duration of the actual stress, either of these two types of plants will emerge as the one having a better competitive advantage (Davies and Gowing, 1999). This will then influence, within the limits of physiological plasticity, their success in the plant community [See Section 5].

4.2 Plant adaptations to water stress

Plants respond to water stress in two ways: by avoidance of the stress or by tolerating it. Stress avoidance is accomplished when plants alter their growth schedule to escape the exposure to damaging stress. Well known examples in this category include completing the life cycle while conditions are optimal, or using strategies to maximize water uptake from the environment and or conservation. On the other hand the tolerance response to water stress occurs when plants develop certain characteristics, often of biochemical and or morphological nature, to minimize the potential damage from stress. An example of the latter could be additions to photosynthetic pathways such as Crassulacean Acid Metabolism (Scott, 2000) for drying stress. Some morphological adaptations for flooding stress include and development of air-space tissue (aerenchyma) within tissues and ventilation roots (pneumatophores). The development of the ability to metabolize products of anaerobic respiration and tolerate an accumulation of anaerobic metabolites is also another biochemical adaptation utilized by wetland plants.

As a closing remark to this section, it is worth mentioning, an extreme form of adaptation to water-deficit by a group of plants known as Poikilohydrics or resurrection plants. Poikilohydric plants show an ability of mature tissues such as the shoot, stem and leaves to tolerate almost complete dehydration of the tissues and then return as functional units very rapidly on rehydration, sometimes in as short as 24 hours (Norwood, *et al.* 2003). Obviously, such plants are native to and inhabit ecological niches that are subjected to lengthy periods of drought with brief periods of rain during the year e.g. deserts of Southern Africa, Southern America and Western Australia (Scott, 2000).

5. Distribution of plants in response to water regime

Differences in water regime have been known to be behind existence of different vegetation types and ecosystems. Some widely known examples include global and regional distribution of plant communities. At global level examples include the major world biomes, such as tropical rainforest, deserts and tundra. At this level, precipitation differences as a result of latitude and incoming solar radiation define certain plants to prevail. A regional example is where plant communities are defined by precipitation differences associated with topographic features, such as elevation. A well known such example being a study as given in Figure 1. The distribution of plant species in relation to water regime at regional level, had been examined using the subjective Ellenberg values, developed from field observations by the eminent German botanist, Heinz Ellenberg.

However, only recently has been the potent role of fine-scale heterogeneities in hydrology on a plot scale identified as principal driver for the defining structures in plant communities (Silvertown *et al.*, 1999). These fine-scale differences in hydrological regime accomplish this structuring by creating realized niches, which are capable of being exploited by specific species. This is illustrated in Figure 4, with hydrological niches of 8 species of sedge in UK wet meadows.

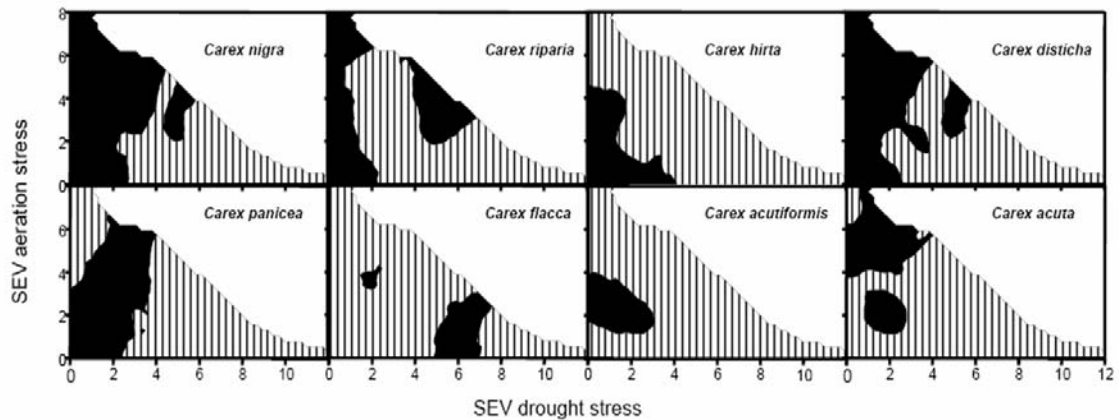


Figure 4. Distributions of 8 sedge species showing differentiation in niche space defined by hydrological axes on a fine-scale gradient. The x-axis depicts increasing soil drying stress, while the y-axis shows increasing flooding (*i.e.* aeration) stress [See section 3 for explanation]. The vertically hatched area in each graph shows the range of possible hydrological regimes and the solid area indicates the zone in which the species occurs significantly more frequently than by chance. Data are cumulated across 18 different meadow sites (after Gowing *et al.*, 2002).

As a conclusion the ecology of plant water relations is explained by the different hydrological niches exploited within coexisting species of a community. These niches are a result of distinct plants' differing physiological response to water stress and presence of other neighbouring plants.

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GLOSSARY

Ellenberg scores: Ellenberg scores are subjective indices relating plant distribution and environmental factors. Ellenberg values were developed by the eminent German botanist Heinz Ellenberg from extensive field observations. Ellenberg scores for soil water availability range between 1-12, where for e.g. 2 indicates a plant adapted to very dry site while 10 indicates a plant adapted to very wet soils.

Niche: The range of environmental conditions (biological and physical) under which an organism exists. An organism may occupy a narrower range of niche under conditions where other competitors exist. **Hydrological niche** is a niche stratified mainly as a result of soil water availability.

Soil texture: Soil texture is a soil physical property used to describe the relative proportion of different grain sizes of mineral particles in a soil. According to size these mineral particles are classified as sand, silt and clay. The arrangement of individual soil particles and the particular way they aggregate is called **soil structure**.

Sum Exceedence Values (SEV): is a hydrological niche metric that defines the degree of soil drying and waterlogging (aeration-stress) by cumulating periods when the water level falls below 5 kPa, a threshold at which soil moisture tension could induce stomatal closure (SEV dryness) and SEV for aeration stress (SEV aeration), when water level results in < 10% air-filled pore-space that limits the free diffusion of oxygen in the topsoil. The thresholds are developed specifically for each soil type encountered and hence once calculated are transferable between different sites.

Water-deficit: Water-deficit refers to a state of the soil when a large proportion of soil pores are occupied by air and not water. Moreover it signals the point when plants start suffering the consequences of reduced water supply. Water deficit usually happens once gravitational water has drained off.

Waterlogging: When all the pore spaces in the soil are occupied by water waterlogging occurs. Under such conditions diffusion of oxygen and gas exchange is reduced between plants and the soils as well as the atmosphere.

Water potential: Water potential is a concept used to evaluate the water status of soils and plants. Water potential refers to the free energy of water, or more technically the amount of energy required to move 1 mole of pure water at ambient temperature and pressure to another state at the same conditions. Water potential is expressed in units of pressure, of which kilopascals (kPa) is most frequently used.