Substrate Effects on Plant Transpiration Rate under Several Vapour Pressure Deficit (VPD) Levels

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Abstract
Vapour pressure deficit (VPD) is considered as an important environmental factor that affects transpiration rate (TR) in plants. VPD is the difference between the amount of moisture in the air and the amount of moisture the air can hold when saturated. Since VPD increases, the drying ability of air increases. Plants transpire more, requiring more water to be drawn from the roots. As the guinea grass are well adapted in various types of soils, therefore in this study, Panicum (Panicum maximum cv. tanzania) was used with 4 different substrates (hydroponic, organic, sand and mineral) subjected to low (0.50-1.50) and high VPD (2.50-3.90) environments to study their substrate effects on plant transpiration rate in 3 different growth stages (31, 37 and 43 DAS for organic, sand and mineral soil and 25, 31, 38 days for hydroponic respectively). The highest transpiration rate of Panicum was measured in hydroponic condition (5.44) under higher VPD level and lower leaf area. The lowest TR measured in sandy soil (0.17) with lower VPD level and large leaf area.

The results showed that sand substrate has the lowest transpiration rate and hydroponic condition showed highest transpiration rate. Other substrates rate in between two of them. However, the results showed that overall transpiration rate was significantly decreasing along the growth stages. Adding more substrates and tying a small around all the exposed leaves would be the way to obtain the exact amount of water transpired from the water source, which makes the results more comparable among the substrates.

Keywords: Vapour pressure deficit; Transpiration rate; Water use efficiency; Days after sowing; Water holding capacity; Crop per drop; Evaporation; Evapotranspiration

Introduction
Panicum maximum (guinea grass) preferably grows in tropical and subtropical areas of the world on a wide variety of soil [1]. Motta [2] also reported that Guinea grasses are well adapted to a wide range of soils. It is tolerant to light frost and low soil pH [3]. Cook et al. [4] also mentioned that guinea grasses are drought tolerant and they can survive a shortage of water.

VPD is a good indicator of plant stress, brought about by either excessive transpiration of water (high VPD values) or the inability to transpire adequately (low VPD values). Vapor pressure deficit is the difference between the vapor pressure at ambient conditions and the vapor pressure at saturation point for the same temperature. Because saturation vapor pressure increases exponentially with temperature, VPD increases with temperature exponentially if absolute humidity is held constant. Therefore, temperature and vapor pressure deficit (VPD) effects on plant growth are usually confounded [5]. Increasing VPD rates raise up the atmospheric demand and consequently higher plant transpiration. Stomatal closure limits the transpiration rate and sometimes a decrease at high VPD [6]. Therefore, stomatal closure restricts the corresponding decrease in plant water potential and prevents excessive water loss.

The characteristics of soil play a significant role in the plant’s ability to extract water and nutrients. If plants are to grow to their potential, the soil must provide a satisfactory environment for plant growth. Water holding capacity is also dependent on soil texture and the effects of soil organic matter are strongest in more sandy soils [7-9]. Texture, structure and porosity influences the movement and retention of water, air and solutes in the soil, which subsequently affects the plant [10].

Hazelton and Murphy [11] indicated that root growth can be severely restricted well before that value of resistance is reached. Because of the links to soil porosity, there is a strong interaction between soil structure, aggregate stability, bulk density and water holding capacity [7,12,13]. Most of the studies have been conducted in a specific growth phase of the crop while there is little information on transpiration rate over the plants ontogeny, but this study has been conducted for checking the substrate effects on plant transpiration rate at different growth stages.

The original intent of this experiment was to study the effect of transpiration rate, as manipulated by several vapor pressure deficit levels in combination with different substrates. To check how the soil response against soilless culture and other soil types with their different time frame in term of water transpiration. Transpiration response may depend on their soil structure, texture, water holding capacity and many other soil properties.

Objectives
The overall objective of this thesis is:

- To assess the effects of soil substrates at different growth stages on plant transpiration rate under variable vapour pressure deficit (VPD) levels.

Further objectives for this research are:

- To describe how environmental conditions alter the rates of transpiration

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To compare the behaviour of soilless panicum crop transpiration with other substrates during ontogeny

**Hypothesis**

The hypotheses are

- Substrates have the effects on transpiration rates at lower (0.50-1.5) and higher (2.50-3.90) VPD levels
- Transpiration rates may affect by growth stages

**Materials and Methods**

The experiment was carried out during the summer season under greenhouse conditions (22-35°C; light: dark = 16:8 hours). Roose [14] also noted that guinea grass can easily be cultivated from seeds and it grows rapidly and occurs in abundance in veld that is in a good condition. In this study seedlings were grown on four different substrates in greenhouse and brought into computer controlled climate chambers for measuring the transpiration rates.

**Plant material**

Panicum seeds (*Panicum maximum cv. tanzania*) were used to grow for seedlings in green house in different substrates. The panicum plants are tufted perennial, drought tolerant and adapted on a large range of soils, but produces poor stands on infertile types [15]. The upper floret (seeds) was collected from Brazil.

**Plants growing strategy**

- The whole experiment was split into three sub divisions
- Panicum plants were raised in four (hydroponic, organic, mineral and sand) different conditions in controlled environments
- Transpiration rates were measured in the climate chamber and biomass harvested
- Water protocol establishment for effective water use

**Substrates and its properties**

Guinea grass was raised in four different (hydroponic, organic, mineral and sand) conditions in controlled environment. Each substrates has different properties (Table 1).

**Seeding were raising in four different conditions**

Guinea grass was growing in four different substrates. Five seeds of *Panicum maximum cv. tanzania* were placed in three (mineral, sand

<table>
<thead>
<tr>
<th>Species</th>
<th>Substrates Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Panicum maximum cv. tanzania</em></td>
<td>- Organic soils (soil with more than 20% organic carbon content)</td>
</tr>
<tr>
<td></td>
<td>- Fine textured soil</td>
</tr>
<tr>
<td></td>
<td>- High water retention capacity</td>
</tr>
<tr>
<td></td>
<td>- Less able to retain nutrients</td>
</tr>
<tr>
<td>Sand</td>
<td>- Low water holding capacity</td>
</tr>
<tr>
<td></td>
<td>- Sand tends to have large particles (2.0 mm -0.05 mm)</td>
</tr>
<tr>
<td>Mineral</td>
<td>- Derived from minerals or rocks and containing little humus or organic matter</td>
</tr>
<tr>
<td></td>
<td>- Less than 20% of organic carbon</td>
</tr>
<tr>
<td>Hydroponic system</td>
<td>- pH was maintained 5.5</td>
</tr>
<tr>
<td></td>
<td>- Nutrient mixed solution</td>
</tr>
<tr>
<td></td>
<td>- Each of the containers contain 8 panicum plants</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Substrates</th>
<th>Soil weight (g) after drying</th>
<th>Saturated weight (g)</th>
<th>Weight until final drop exit</th>
<th>WHC (%)</th>
<th>Targeted weight (g) with 75% moisture</th>
</tr>
</thead>
<tbody>
<tr>
<td>Organic</td>
<td>450</td>
<td>304.2</td>
<td>815</td>
<td>338</td>
<td>141.12</td>
</tr>
<tr>
<td>Sand</td>
<td>1000</td>
<td>904.77</td>
<td>1878</td>
<td>1508</td>
<td>24.56</td>
</tr>
<tr>
<td>Mineral</td>
<td>800</td>
<td>774.93</td>
<td>1985</td>
<td>1380</td>
<td>43.84</td>
</tr>
</tbody>
</table>

**Table 2:** Fixed amount of water calculation for 75% moisture in each and every pot.

**Technical set-up for hydroponic system**

Figure 2 showing the panicum plants were growing in hydroponic system. Two similar sized containers with thirty liters of nutrient mixed (Table 2) distilled water was used for growing plants. Two bubble plates were placed at the bottom of the container for uninterrupted oxygen supply. A clock was placed to indicate every 15 minutes interval. Two weeks aged Panicum seedlings were transplanted to the hydroponic containers from other substrates. Each of the containers raised eight Panicum plants. After twenty-three and twenty-four days from the sowing, the extra nutrient (1 ml per liter, Table 2) was mixed and normal distilled water was added to the container to compensate for the loss by plants and evaporation. The pH was maintained at (5.5) by adding 0.5M HCl since the Panicum can absorb a high amount of nutrient from the nutrient mixed solution.

**Technical set-up for climate chamber**

The plant transpiration rate was measured in a climate chamber (80x80x100 cm) with PVC transparent side and top elements. LED light was installed 15 cm away from the top of the climate chamber.

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for providing photosynthetic photon flux (PPF) at 600 μmol m⁻²s⁻¹ at the bottom and 1200 μmol m⁻²s⁻¹ near the top. Uninterrupted airflow through the VPD chamber excluded the possibility of carbon dioxide deficit in the chamber. The temperature and the relative humidity were recorded every minute for calculating the accurate atmospheric VPD by using Tinytag data loggers (Type-TV4505, Gemini Data Loggers., UK). Four individual balances (KERN KB 2400-2N d=0.01 g, with a maximum load of 2400 g) arranged symmetrically in order to maintain equal light conditions which are connected to a PC for every minute weight information with GrassLog software version 0.1. Four box fans are installed on the top of the chamber for mixing the inside air by continuously adjustable intensity.

A desiccant dehumidifier (Consorb DC-10, Seibu Giken, Sweden) was used to generate dry air at a flow rate of max. 190 m³/h. The air flow at 60 m³/h was simultaneously used to counterbalance temperature losses of the wet air produced by ultrasonic nebulizers (Fogstar 100, Seliger GmbH, Germany). Both air streams were saturated before entering the chamber from a side entrance. The speed of each air stream was adjustable with throttle flaps placed inside PVC tubes before mixing.

The actual atmospheric VPD was measured by calculating the recorded every 60 sec relative humidity and temperature. Different humidity levels were reached by adjusting throttle flaps of wet and dry airstreams while targeting five VPD levels between 0.5 and 3.9.

**Plant transpiration rate measuring in the climate chamber**

Figure 3 showing the transpiration rate measurement in climate chamber. During the measurements of transpiration in the chamber, the pot was covered with aluminum foil to eliminate evaporation from the growth medium. Initially, VPD was maintained approximately 0.5 kPa and increased stepwise to approximately 3.9 kPa. Once the environment in the chamber was equilibrated, the entire unit of plants and pot were weighed on a balance. Steady-state plant transpiration rates were recorded based on the mass loss. Four to five humidity levels in the chamber were established by adjusting the humid and dry air. Measurements were started from low VPD to higher VPD levels to avoid any influence of exposure to high VPD on subsequent VPD measurements. Transpiration rates were recorded over 20 minutes for each VPD levels with an interval of 10 minutes for adjusting VPD until the starting of the higher VPD levels. The measurements for each replicate consisted of five VPD levels for around 3 hours in total.

**Determination of transpiration rate and dry biomass**

After measuring the transpiration rates in the chamber, the plants were clipped at the stem base and separated into shoot and root. The total leaf area was measured by using LI-3100 area meter. Every substrate was immersed in water to remove sand and soil. Roots were further washed and sealed separately in leveled paper bags. All plant tissues were dried in an oven at 70°C for 48 hours to constant weight.

**Water protocol establishment for effective water use**

A fixed amount of different types of soil (sand 1000 g, mineral 800 g and organic 450 g) were weighed for each substrate and dried it at 75°C temperature for 48 hours. Pots weight was calculated with 75% moisture (Table 2).

Plant water was determined by quantifying their pot weight losses on a daily basis. All pot was weighted every evening before and after watering. Their weight difference was considered as the total daily water use by the plant. Plant biomass was determined at the end of the experiment by cutting leaves, stems and the water cleaned roots and dried in an oven at 70°C temperatures to obtain dry weight. Calculation details can be found in Appendix 1.

**Statistical calculation**

- **Transpiration rate calculation**: Plant transpiration rates (TR) were calculated per unit of leaf area (mmol H₂O m⁻² s⁻¹), based on their pot weight changing in every minute’s interval.
  
  \[ \text{TR} = \frac{(W₀-W₁)/18}{\text{Time} \times \text{Leaf Area}} \]

  - W₀ = the initial weight
  - W₁ = weight after 60 seconds

- **Biomass calculation**: Leaf area was measured per (cm²), shoot and root dry weight were measured per (g). The data were analyzed by plotting leaf area, shoot and root dry weight against days after sowing by using statistical software package SAS.

  - **Root-shoot ratio calculation**: Root dry weight (g) was divided by Shoot dry weight (g) in each and every replication.
  
  \[ \text{Root-Shoot ratio} = \frac{\text{Root dry weight (g)}}{\text{Shoot dry weight (g)}} \]

  - **Calculation of water loss by transpiration and evaporation**: The water loss was measured by the weighting of pot weight with panicum plants and without panicum plants.

- **Normalizing transpiration rate to VPD**

In this study, VPD in the chamber were manipulated by manually through adjusting the relative humidity while keeping the temperature constant, therefore, the exact VPD couldn’t be fixed at exactly 0.6, 1.30, 2.0, 2.90, 3.70 kPa. All the TR values were plotted against their respective VPD levels to produce regression line compare with TR and VPD levels with their different substrates and growth stages.

**Results**

**Root-shoot ratio**

Table 3 showed that, the highest amount of root-shoot ratio in hydroponic system in growth stages one and two. In growth stage three, it is higher in mineral soil. The lowest root-shoot ratio was observed in sandy soil in growth stage one and two but in growth stage three its lowest in organic soil.

**Cumulative biomass production by effective water use**

Regression equations can be found in Appendix 2. The analysis
of covariance of the different substrates (mineral, organic and sand) yielded a significant effect of the substrates depending on the water uptake across the growth stages (p-value = 0.0115). In the first growth stage, there is a strong increase in the leaf area growth for sand substrate (0.57 cm² per 1 ml water), followed by the mineral substrate (0.31 cm² per 1 ml water). The organic substrate does not show an important increment of the leaf area (0.01 cm² per 1 ml water) (Figure 4, equations 01, 02, 03). In the second growth stage, the mineral substrate continued growing (0.23 cm² per 1 ml water), whereas substrates organic and sand did not register a significant increase in leaf area (Figure 4, equations 04, 05, 06). In the last growth stage, substrates had similar behavior with relevant increments among the substrates (Figure 4, equations 07, 08, 09).

<table>
<thead>
<tr>
<th>Substrates</th>
<th>Growth stage 1</th>
<th>Growth stage 2</th>
<th>Growth stage 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>organic</td>
<td>0.4136</td>
<td>0.5522</td>
<td>0.4754</td>
</tr>
<tr>
<td>sand</td>
<td>0.4118</td>
<td>0.4861</td>
<td>0.4867</td>
</tr>
<tr>
<td>mineral</td>
<td>0.4463</td>
<td>0.5089</td>
<td>0.4891</td>
</tr>
<tr>
<td>hydroponic</td>
<td>0.5369</td>
<td>0.5666</td>
<td>0.4777</td>
</tr>
</tbody>
</table>

Note. Calculation details can be found in Appendix 1

Table 3: Root-Shoot ratio (root dry weight (g) / shoot dry weight (g)) in four substrates in three different growth stages (31, 37 and 43 DAS for organic, sand and mineral soil and 25, 31, 38 DAS for hydroponic respectively).

Transpiration rate and substrates effects

Polynomial regression of transpiration on vpd was performed at each growth stage. At growth stage one a significant Linear increase of transpiration with increasing vpd was found (p<0.0001). Transpiration rate was higher in hydroponic system followed by mineral substrates with their different vpd levels (Figure 5). At growth stage two a significant quadratic increase of transpiration with increasing vpd was found (p<0.0001). Organic and sandy soil indicated lower transpiration rate in early stages. The hydroponic system showed that transpiration rate was higher than the other substrates in growth stage two (Figure 6). Transpiration rate was lower in sandy soil with their low and high vpd. At growth stage three a significant Linear increase of transpiration with increasing vpd was found (p<0.0001). Transpiration rate continued higher in a hydroponic system in the final growth stage and statistically similar transpiration rate among the other substrates (Figure 7). The range of transpiration rate was gradually decreasing from the first to final growth stage (Figures 5-7).

Discussion

Plants biomass and transpiration rate

We emphasize that the leaves are the final frontier of the water flow in the continuous soil-plant-atmosphere system. The plant, which is an
intermediate in this process, may regulate the water potential gradient between the soil and the atmosphere primarily through the regulation of stomatal conductance. But results showed that the transpiration rate was gradually decreasing with their growth stages (Figures 5-7) and this effects supported the second hypothesis which was transpiration rates has growth stages effect.

The rate of water supply to the plant shoot is dependent on both the conductance of water in the soil and in the roots [16,17]. In that case, the hydroponic system has the huge possibility for water and root conductance than the other substrates followed by organic soil and mineral soil. The fine textured soil has the more ability to preserve and continuous water supply around the root zones compare to the sandy soil. In that case, organic soil generated higher root volume and transpired more water than the sand in the final growth stage.

Root-shoot ratio

The rate of transpiration tends to increase with higher root-shoot ratio [18]. He also mentioned that it is expected that a plant with a higher root: shoot value will tend to transpire faster than another plant with a lower root to shoot. In this experiment it’s clearly observed that, the root-shoot ratio was higher in the hydroponic system in growth stage one and two and plants transpired more water compared to the other substrates (Table 3).

Soil properties in terms of transpiration rate

Soil texture and structure greatly influence water infiltration, pH, permeability and water holding capacity. Soil texture refers to the composition of the soil in terms of the proportion of small, medium and large particles (clay, silt and sand respectively) in a specific soil mass. Soil structure refers to the arrangement of soil particles (sand, silt and clay) into stable units called aggregates, which give soil its structure. Aggregates can be loose and friable or they can form distinct, uniform patterns. Brady [19] mentioned that sandy soils have low porosity and the movement of air and water is rapid. Soil porosity refers to the space between soil particles, which consists of various amounts of water and air. A fine soil has smaller but more numerous pores than a coarse soil. A coarse soil has bigger particles than a fine soil, but it has less porosity or overall pore space.

Smettem and Collis-George [20] reported that a single continuous pore of 0.3 mm diameter can conduct more water than the rest of a 100 mm diameter sample. Water can be held tighter in small pores than in large ones, so fine soils can hold more water than coarse soils. In that case, available water was higher in organic and mineral soil and transpires more water than the sandy soils (Appendix 3).

Gardner [21] also reported that, where a shallow water table is present, more rapid evaporation may continue indefinitely if the unsaturated conductivity of the soil at the surface is sufficient to sustain unsaturated flow from the water table. In this study, sandy soil evaporated higher amount of water than the other substrates. Probable cause may be the available plant water and the water holding capacity is lower in sandy soils (Appendix 3) [22].

Naiman et al., [23] also mentioned that higher levels of organic matter result in a greater number of cation exchange sites which tend to decrease the pH. He also indicated sandy soils with a low CEC are generally unsuited for septic systems since they have the little adsorptive ability and there is potential for groundwater. The main effect of soil pH is on the availability of plants nutrients which have the specific preference range of soil pH. In these studies pH 5.5 has been maintained for hydroponic growth system but the other substrates pH was unknown. So pH could be varied and it might have the effects on nutrients absorption, even extra nutrients was supplied in sand and mineral growth medium for equal plant growth but the effects still unclear.

**Cumulative biomass production by effective water use and transpiration rate**

In this study, transpiration difference was isolated by comparing similar size individual pot weight in each plant at each growth stage. Accept hydroponic condition (full of water with nutrients, Appendix 4), results showed that organic substrate used a significant amount of water by generating the shoot biomass in final growth stages compared to the other growth medium (Figure 4).

Seckler [24] introduced the expression ‘more crop per drop’ to mean that increasing crop water productivity was more relevant than just saving water. Since biomass production is tightly linked to transpiration, crop per drop can be estimated by calculating the generated per unit leaf area by the amount of water transpired.

In this study, it has been done by measuring the quantity of water directly transpired from the crop, i.e. the transpiration efficiency, the quantity of water lost through soil evaporation (Appendix 3) and productivity per unit of water applied, i.e. irrigation efficiency (Figure 4). Results showed that organic substrates used more water or transpired higher amount of water than the sand substrates but generated less leaf area (Figure 4). A number of tillers and easy root penetration in the sand could be the result. Or it may effect of additional nutrients supply (1 ml per liter water, Appendix 4) and rooting volume.

In this study, the amount of transpired water by evaporation was higher in sandy soil in each and every growth stage (Appendix 3), because of their large particle size (>0.05 mm) which tend to fit loosely together. In contrast, clay particles are much smaller and fit together more tightly in the soil. So they’re more resistant to the force of gravity that pulls water quickly through the sandy soil.

Acar [25] have demonstrated the electroosmotic component of transport may disappear in coarse sands and high plasticity clays at low water contents. They also indicated that organic material can hold onto nutrients electrochemically and because clay soils are better able to hold onto organic matter than sandy soils. The advantage of clay over sand in terms of nutrient retention ability is enhanced even further. In that case, plants have taken up a large amount of water in organic substrates in growth stage three (Appendix 3).

However Trejo and Davies, [26] reported that the physiological response of the plant shoot to soil drying results from hydraulic or chemical signals is as yet unclear.

**Conclusion and Outlook**

The experiment of transpiration consisted of testing how fast different types of substrates plants can transpire water from their leaves. In this studies, its shows gradually reduction in the foliar transpiration rate of guinea grass over its ontogeny under lower to higher VPD levels. Although little or no change in biomass production was shown in this study, differences were observed in overall plant leaf area under low and high VPD levels. But the results showed that leaf area expansion is a key difference of guinea grass to high VPD. The Panicum plants showed a negative relationship between changes in TR and leaf area expansion under high VPD and growth stages. That is, under high VPD, higher TR was associated with lower leaf area expansion rates as shown in the results. Transpiration rate is higher in hydroponic...
condition than the other substrates in Panicum from lower to higher VPD and the lowest in sand accept 1st growth stage. Significant effects of transpiration rate in different VPD were observed in each substrate across their growth stages.

Including by more substrates and growth stages would be the preference for further research. Checking the rewetting data could be the possible way to know plant recovering. Tying a small around all the exposed leaves would be the way in order to obtain the exact amount transpired from the water source into the atmosphere. This will be able to provide more details on the exact time and amount of how much water was transpired. It will override the possibility and time lag of water not yet transpired, but counted as so due to its absence in the pots.

Acknowledgment

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References