Plant identity and shallow soil moisture are primary drivers of stomatal conductance in the savannas of Kruger National Park

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Abstract

Our goal was to describe stomatal conductance ($g_s$) and the site-scale environmental parameters that best predict $g_s$ in Kruger National Park (KNP), South Africa. Dominant grass and woody species were measured over two growing seasons in each of four study sites that represented the natural factorial combination of mean annual precipitation [wet (750 mm) or dry (450 mm)] and soil type (clay or sand) found in KNP. A machine-learning (random forest) model was used to describe $g_s$ as a function of plant type (species or functional group) and site-level environmental parameters (CO$_2$, season, shortwave radiation, soil type, soil moisture, time of day, vapor pressure deficit and wind speed). The model explained 58% of the variance among 6,850 $g_s$ measurements. Species, or plant functional group, and shallow (0–20 cm) soil moisture had the greatest effect on $g_s$. Atmospheric drivers and soil type were less important. When parameterized with three years of observed environmental data, the model estimated mean daytime growing season $g_s$ as 68 and 157 mmol m$^{-2}$ sec$^{-1}$ for grasses and woody plants, respectively. The model produced here could, for example, be used to estimate $g_s$ and evapotranspiration in KNP under varying climate conditions. Results from this field-based study highlight the role of species identity and shallow soil moisture as primary drivers of $g_s$ in savanna ecosystems of KNP.

Introduction

Stomatal conductance ($g_s$) is a measure of gas exchange between plants and the atmosphere. Stomatal conductance is an important component of water and CO$_2$ cycles at both local and global scales [1,2,3]. For example, the $g_s$ models developed by Jarvis [4] (including subsequent Jarvis-type models [5] and Ball, Berry, and Woodrow models [6]) are widely-used to estimate canopy-level processes and global circulation of atmospheric gasses [7,8]. These models of $g_s$ are empirical, but have been integrated with more mechanistic models that are founded on a sound understanding of the cellular and leaf-level drivers of $g_s$, such as CO$_2$ concentration, irradiance, and vapor pressure deficit (VPD) [2,7,8,9,10].

While $g_s$ is fairly well understood at the cellular and leaf level, it is less understood at the landscape scale where factors such as species identity, soil moisture, disease, plant age and...
interactions among these factors can affect $g_s$ [1,2,5,9,11]. One central problem for understanding landscape-scale $g_s$ is that the field-based datasets used to build and validate models are typically small (i.e., several 100 measurements) or are inferred from ecosystem flux or sap-flux measurements [10,12,13,14]. Small $g_s$ datasets are unlikely to capture the variability in $g_s$ that occurs among species, within canopies, and over daily and seasonal time-scales in response to environmental drivers [13,15,16,17]. Without large field-based datasets, it is difficult to know which parameters are of primary importance to $g_s$ under field conditions [10,14,18,19].

There is a particular need for understanding $g_s$ in savanna ecosystems [16,20]. Savannas are defined by codominance of grasses and woody plants that may vary widely in abundance and also in their $g_s$ responses to environmental drivers [10,12,21]. Further, because savannas are geographically extensive and because savanna $g_s$ responses are likely to be sensitive to changes in climate and human management (e.g., grazing and fire suppression), these systems are likely to have important impacts on global scale biosphere-atmosphere feedbacks [1,22].

As in most ecosystems, $g_s$ in savannas has been observed to decrease with VPD and soil moisture [23,24], have a saturating increase with light intensity [10,23] and a unimodal response to temperature [12]. However, soil moisture in these semi-arid systems may have an overriding effect on $g_s$ [10,12,25]. Further, different precipitation regimes and seasonal responses to these precipitation regimes have been found to affect how plants exercise stomatal control [26,27]. Species identity may also be critical to understanding $g_s$ in savannas. Grasses are likely to have shallower rooting profiles, making them more sensitive to within-season droughts [28,29,30]. Similarly, $g_s$ of grasses using the C4 photosynthetic pathway have been found to be highly sensitive to water stress [31] (though at least one study has failed to detect differences between C4 grass and C3 woody plants in a West African savanna) [23]. Further, grasses are likely to realize different environments than their woody plant counterparts because short, dense grass canopies are decoupled from the above-canopy atmosphere and because grasses occur both underneath and between tree canopies [32].

While leaf-level models of $g_s$ focus on the roles of $[\text{CO}_2]$ and VPD [10], we predicted that variation in landscape-level $g_s$ in a sub-tropical savanna will be best explained by soil water availability and plant type. This is because soils often dry during the growing season in semi-arid systems and dry soils can induce stomatal closure regardless of $[\text{CO}_2]$ and VPD. We predicted that species effects will be important because grasses and woody plants co-dominate savannas and differ in their rooting patterns [30,33].

The overarching goal of this study was to describe site-scale $g_s$ in the savannas of Kruger National Park (KNP), South Africa. Because the 19,485 km$^2$ KNP encompasses a range of precipitation regimes [from 450 to 750 mm mean annual precipitation (MAP)] and soil types (clay and sand), measurements were made in four sites that represent the natural factorial combination of precipitation (wet or dry) and soil type (clay or sand) found in KNP [34]. More specifically, our objectives were to 1) develop a dataset large enough to describe $g_s$ across the four dominant bioclimatic areas found in KNP, 2) use the dataset to build a statistical model of $g_s$ as a function of environmental drivers and 3) use the model to produce continuous estimates of grass and woody plant $g_s$ using three years of observed environmental data.

**Materials and methods**

**Study site**

This study was performed in KNP and was approved by the South African National Parks (project registration number 213896412). KNP is located in north-east South Africa between 30.9°–32.0° E and 22.3°–25.5° S. It is characterized by hot, wet summers (October through May)
and cool, dry winters (June through September) [34]. A rainfall gradient from north to south in the park produces a range of mean annual precipitation (MAP) from 450 mm to 750 mm yr\(^{-1}\), which is representative of a large proportion of precipitation-limited savannas [34,35,36]. Most of the eastern half of KNP is underlain by basaltic rock that weathered into nutrient-rich, clay-rich soils, while the western half is underlain by granitic rock that weathered into nutrient-poor, sandy soils [37]. Four study sites were selected that represented a natural factorial combination of precipitation regimes (“wet” or “dry”) and soil texture (“sand” or “clay”; Table 1) [38] found in the park. The four sites occur on very gently rolling to flat terrain. Water infiltration occurs through the top 1 m of soil within a few days of large, mid-season precipitation events at all sites, but little water infiltrates below this rooting zone [30,39,40]. Even if total annual precipitation occurred as a single event, it would be expected to saturate soils to 3.0 to 3.7 m in the different sites.

The four study sites are typically dominated by one to three woody plant species and one to three grass species [34]. Dominant C4 grasses at the four sites were *Bothriochloa radicans* (Lehm) A. Camus, *Schmidlia pappophoroides* (Steed.), *Urochloa mosambicensis* (Hack) Dandy and *Cenchrus ciliaris* L. at the dry/clay, dry/sand, wet/clay and wet/sand sites, respectively. Dominant woody plants were *Colophospermum mopane* (Kirk ex Benth.) at the dry/clay and dry/sand sites, a mix of *Securinega virosa* (Roxb.), *Strychnos spinosa* (Lam.) and *Dalbergia melanoxylon* (Guill. and Perr.) at the wet/clay site and *Sclerocarya birrea* and (A. Rich) and *Terminalia sericea* (Burch ex. DC) at the wet/sand site.

### Study design

**Stomatal conductance measurements.** The four sites were each sampled during two different seasons (Table 1). During each season, measurements were made over two to three days during two early- (November, December), two mid- (January, February) and two late-season (March, April) sampling periods. As a result, \(g_s\) was measured on 24 to 36 different days at each site. During each sampling day, one to four people with a list of target species and a steady-state porometer (Decagon Devices, SC-1) [41], would walk along a transect until they encountered one of four to nine target species (Table 2). The number of target species was selected so that sampled species represented 80% of total leaf area at a site. Leaf area was determined in separate research using 96, 1-m\(^2\) quadrats [30,33]. Measurements were taken throughout the plant canopy. For grasses, measurements were made near the end and near the base of leaves on both adaxial and abaxial surfaces. For woody plants, only abaxial measurements were detectable. Woody plant leaves were sampled from top, middle, bottom and inner canopy positions roughly proportionate to their abundance. Target species would be sampled within 15-minute increments of either consistently clear or consistently overcast conditions. After collecting samples from the target species for a site, additional time in the 15-minute increments was used to take extra samples from the most dominant species. Measurements

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**Table 1. Precipitation regimes, soil types and sampling seasons corresponding to the four study sites in Kruger National Park, South Africa.** Growing seasons occur from October through May and are referred to by the year during which the growing season ends.

<table>
<thead>
<tr>
<th>Site Name</th>
<th>Precipitation Regime</th>
<th>Soil Type</th>
<th>Season Sampled</th>
</tr>
</thead>
<tbody>
<tr>
<td>Letaba</td>
<td>dry (450 MAP(^*))</td>
<td>clay (calcareous shallow clay)</td>
<td>2010, 2013</td>
</tr>
<tr>
<td>Phalaborwa</td>
<td>dry (475 MAP)</td>
<td>sand (coarse fersiallitic sand)</td>
<td>2011, 2012</td>
</tr>
<tr>
<td>Lower Sabie</td>
<td>wet (730 MAP)</td>
<td>clay (pedocutanic clay)</td>
<td>2011, 2013</td>
</tr>
<tr>
<td>Pretoriuskop</td>
<td>wet (750 MAP)</td>
<td>sand (coarse fersiallitic sand)</td>
<td>2008, 2009</td>
</tr>
</tbody>
</table>

\*MAP = Mean annual precipitation in mm.

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were made to be roughly representative of species abundance and at the end of the study the number of gs measurements per species was positively correlated with leaf area by species ($R^2 = 0.66$). Samples were taken between sunrise and sunset, though few measurements were taken at dawn and dusk due to safety concerns of working in the park.

**Environmental parameters.** Temperature, relative humidity (215L; Campbell Scientific, UT, USA), wind speed (014A cup anemometer; MetOne, OR, USA) and shortwave radiation (SP-110; Apogee Instruments, UT, USA) were measured at 1 m and 2 m heights. Measurements at 1 m and 2 m were used for models of grass and tree gs, respectively. Precipitation (Texas Instruments TE-525; Texas Instruments, TX, USA) and soil water potential were measured at one location at each site. All measurements were recorded hourly at each site on Campbell Scientific CR1000 dataloggers. Air temperature and relative humidity were used to calculate VPD. Atmospheric CO$_2$ measurements were provided by a flux tower near Skukuza, which was 32 to 136 km from the study sites [42,43]. Inasmuch, CO$_2$ data provided inference to broad, regional scale patterns and not site-specific patterns of CO$_2$ concentrations. The CO$_2$ sensor was located eight meters above most of the canopy and six meters above the tallest trees in the flux tower fetch [42,43]. Heat dissipation sensors (Campbell 229L; Campbell Scientific, UT, USA) were used to calculate soil water potential hourly for 0–20 cm, 0–50 cm, 20–50 cm, and 50–150 cm depths for each site. Heat dissipation sensors were calibrated individually prior to installation [30,44].

**Data analyses.** Because we sampled across four distinct sites, we first used a one-way analysis of variance to test for differences in mean gs values among sites for each plant functional type (woody plants and grasses). To meet assumptions of normality, gs values were log-transformed. Because sample sizes differed among sites, Type III sum of squares were used and pairwise comparisons were examined using the Tukey test. Species with less than 100 measurements in the dataset were excluded.

**Random forest modeling.** We used a machine-learning model to 1) describe the relationship between environmental parameters and gs, 2) build a predictive model of site-scale gs, and

<table>
<thead>
<tr>
<th>Species</th>
<th>Plant type</th>
<th>Sample Size by Site</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bothriochloa radicans</td>
<td>Grass</td>
<td>DC (456), DS (12), WC (60)</td>
</tr>
<tr>
<td>Cenchrus ciliaris</td>
<td>Grass</td>
<td>WS (458)</td>
</tr>
<tr>
<td>Loudetia simplex</td>
<td>Grass</td>
<td>WS (134)</td>
</tr>
<tr>
<td>Panicum spp.</td>
<td>Grass</td>
<td>DC (11), WC (234)</td>
</tr>
<tr>
<td>Schmidtia pappophoroides</td>
<td>Grass</td>
<td>DS (71)</td>
</tr>
<tr>
<td>Urochloa mosambicensis</td>
<td>Grass</td>
<td>DC (25), DS (76), WC (245)</td>
</tr>
<tr>
<td>Acacia nigrescens</td>
<td>Woody</td>
<td>DS (33), WC (208)</td>
</tr>
<tr>
<td>Colophospermum mopane</td>
<td>Woody</td>
<td>DC (843), DS (178)</td>
</tr>
<tr>
<td>Combretum apiculatum</td>
<td>Woody</td>
<td>DC (12), DS (102)</td>
</tr>
<tr>
<td>Combretum imberbe</td>
<td>Woody</td>
<td>DS (36), WC (68)</td>
</tr>
<tr>
<td>Dichrostachys cinerea</td>
<td>Woody</td>
<td>DS (106), WS (749), WC (402)</td>
</tr>
<tr>
<td>Grewia bicolor</td>
<td>Woody</td>
<td>DS (12), WC (109)</td>
</tr>
<tr>
<td>Lonchocarpus capassa</td>
<td>Woody</td>
<td>DS (15), WS (3), WC (107)</td>
</tr>
<tr>
<td>Sclerocarya birrea</td>
<td>Woody</td>
<td>DC (2), DS (24), WS (148), WC (1)</td>
</tr>
<tr>
<td>Securinga vriosa</td>
<td>Woody</td>
<td>DS (128), WC (298)</td>
</tr>
<tr>
<td>Terminalia sericea</td>
<td>Woody</td>
<td>DS (1), WS (797)</td>
</tr>
<tr>
<td>Ximenia caffra</td>
<td>Woody</td>
<td>WS (106)</td>
</tr>
</tbody>
</table>

https://doi.org/10.1371/journal.pone.0191396.t002
3) estimate site-scale $g_s$ using three years of environmental data. RF models provide the mode or mean of many different classification or regression trees, respectively, and correct for the tendency for decision trees to overfit data [45]. RF modeling reveals nonlinear relationships and complex interactions in ecological data that may be missed by other statistical methods [45].

RF models were used to describe the effect of the following parameters on $g_s$: atmospheric CO$_2$ (ppm), precipitation regime (wet or dry), shortwave radiation (μmol m$^{-2}$ sec$^{-1}$), soil moisture (soil water potential, MPa), soil type (clay or sand), species identity, time-of-day (hour), time-of-season (early, mid, late), VPD (kPa) and wind speed (m sec$^{-1}$). Because $g_s$ can vary widely with plant functional type, and because it is reasonable to expect that grasses and woody plants may respond differently to environmental drivers [46] and because savannas show wide variations in woody plant cover [34,35], $g_s$ was modeled separately for each functional group. Measurements of $g_s$ were paired with meteorological and soil measurements from the closest recorded time step. Where meteorological data was missing for a time step, data were interpolated by correlating and adjusting data from the nearest weather station using a linear equation. Less than 10% of the meteorological data were interpolated. To test for potential lag effects in the response of $g_s$ to environmental conditions, the 3-hour averages of air temperature, relative humidity, VPD, wind speed, and shortwave radiation, the 3-hour, 24-hour, and 7-day averages of each soil moisture depth, and the 24-hour sum of precipitation were calculated and used in the model.

Although highly-correlated predictors do not affect RF variable importance [45], to simplify interpretation of variable relationships, correlation matrices for groups of related predictor variables were used to test for multicollinearity [45]. Air temperature, precipitation, relative humidity, soil moisture, shortwave radiation, VPD and wind speed were evaluated using Spearman correlation. Where two predictors were highly correlated, the predictor with the greatest adjusted-squared-deviance explained by a generalized linear model (GLMs; linear + quadratic, family = Gaussian) was used in the RF model [45]. When highly-correlated predictors explained similar amounts of variance in $g_s$ (difference of less than 2%), separate RF models were created and the variable that explained the most variance was selected.

To estimate the effect that each variable has on model output (i.e., variable importance), values for each variable were randomized, one at a time, and the prediction error in models with randomized and non-randomized values calculated [45,47]. Large prediction error (i.e., variable importance; VIMP) values indicated that specifying the variables incorrectly increased prediction error; therefore, variables with large VIMP values are more important [47].

Relationships between $g_s$ and environmental parameters were characterized with risk-adjusted partial dependence plots [47]. Partial dependence refers to the dependence of the response variable, in this case $g_s$, on one predictor variable [45]. The plots were created by averaging the effects of the remaining environmental parameters and predicting how the response variable changes with the predictor of interest alone [45].

Model estimates of $g_s$ were generated using site-specific data from the 2009/2010, 2010/2011 and 2011/2012 growing seasons. The data were collected and prepared using the same instrumentation and methods as the data used to build the RF models. The data were then run through the RF models using the predict function in the randomForestSRC package [45]. Model estimates were generated separately for each study species present at a site. Average $g_s$ by species (weighted by species abundance) were produced for each plant functional type in each study site and for the entire park. Statistical analyses were performed in RStudio [48]. All RF models and predictions were developed using the R package randomForestSRC [48] and all model visualizations were created using the ggRandomForests package [47].
Results

We present average diurnal environmental conditions from the Pretorioskop site to provide general context of site conditions (Fig 1). Temperature, radiation, VPD, and wind speed all reached maximum average daily values between 16:00 and 17:00 hours at 26.8˚ C, 1491 μmol m^{-2} sec^{-1}, 9.18 kPa and 1.84 m sec^{-1}. Relative humidity realized an average daily minimum at 16:00 hours at 38.3%.

Observed gs

Over the six years of the study, 8,510 g_s measurements were made across the four sites (Table 2). However, 1,080 of these measurements were from species that were measured less than 100 times and were excluded from analyses. Mean observed daytime g_s was 75 ± 1 mmol m^{-2} s^{-1} for grasses and 155 ± 2 mmol m^{-2} s^{-1} for woody plants. Forb g_s was measured for related research and was 142 ± 5 mmol m^{-2} s^{-1}. Because forbs represented < 10% of leaf area and sample size (n = 580), they were excluded from further analyses. Mean observed g_s for grasses was greater in the wet/clay site than the wet/sand, dry/clay or dry/sand sites (Fig 2; F = 28.40, p < 0.001). Mean observed g_s for woody plants was greater in both wet sites than the dry sites and greater in the wet/clay site than the wet/sand sand site and the wet/sand site was greater than either the dry/clay or dry/sand sites (Fig 2; F = 77.30, p < 0.001).

Random forest

With measurements from uncommon species removed, RF modeling was performed on a dataset with 6,850 measurements from common grass and woody plant species. The best RF model for this dataset explained 58% of variance and included, in descending order of importance, species, 24-hour shallow (0–20 cm) soil moisture, 24-hour deep (50–150 cm) soil moisture, 3-hour shortwave radiation, 3-hour VPD, 3-hour wind speed, atmospheric CO_2, time-of-season, time-of-day, precipitation regime, and soil type. This model was used to estimate g_s across three growing seasons (see below). When species was replaced with plant functional type, the percent variance explained by the model decreased to 51% but the order of variable importance remained the same. When neither species nor plant functional type was included in the model, percent variance explained decreased to 40%. Percent variance explained for the grass dataset with and without species was 27% and 21%, respectively. Percent variance explained for the woody g_s dataset with and without species was 54% and 45%, respectively. Remaining analyses were performed separately for grasses and woody plants. Due to multicollinearity, precipitation, relative humidity, 0–50 cm soil moisture, 20–50 cm soil moisture, seven-day soil moisture, three-hour soil moisture, and temperature, were not included in subsequent analyses.

Variable importance. For both grasses and woody plants, shallow (0–20 cm) soil moisture was the most important predictor of g_s, explaining 7 and 10% of the variation in the grass and woody plant datasets, respectively (Fig 3). The remaining variables differed in importance between grasses and woody plants. For grasses, in descending order of importance: VPD, atmospheric CO_2, species, wind speed, shortwave radiation, deep (50–150 cm) soil moisture, time-of-season, time-of-day, soil type, and precipitation regime explained variance in g_s (Fig 3a). For woody plants, in descending order of importance: shortwave radiation, precipitation regime, species, CO_2, VPD, wind speed, deep soil moisture (50–150 cm), time-of-season, time-of-day, and soil type explained variation in g_s (Fig 3b).

In descending order of importance of continuous variables, grass g_s increased 51% with shallow soil moisture, decreased 29% with VPD, increased 22% with CO_2, decreased 16% with shortwave radiation above ~500 μmol m^{-2} sec^{-1}, increased 11% from midday to dusk, and
Fig 1. Average daily values of (a) relative humidity, (b) shortwave radiation, (c) temperature, (d) vapor pressure deficit (VPD), and (e) wind speed over two years at the Pretorioskop study site, Kruger National Park, South Africa.

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showed less than a 10% change with deep soil moisture, shortwave radiation and wind speed (Fig 4; Percentages here represent the difference between maximum and minimum values); Woody gs increased 47% with shallow soil moisture, decreased 18% with VPD values above 0.6 kPa, increased 17% with deep soil moisture, decreased 14% with shortwave radiation values above 500 μmol m$^{-2}$ s$^{-1}$, increased 13% with CO$_2$ and increased 10% with wind speed (Fig 4). Gs differed by more than 10% for only one categorical value: woody gs was 16% greater in wet sites than dry sites (S1 Fig).

**Random forest model estimates of g$_s$.** Mean daytime g$_s$ across three years at the four study sites was 68 and 157 mmol m$^{-2}$ s$^{-1}$ for grasses and woody plants, respectively. Mean estimated g$_s$ was notably greater in the wet/sand site for grasses (78 mmol m$^{-2}$ s$^{-1}$) and woody plants (253 mmol m$^{-2}$ s$^{-1}$) than other sites. Mean estimated grass g$_s$ was 68, 65 and 62 mmol m$^{-2}$ s$^{-1}$ in wet/clay, dry/sand and dry/clay sites, respectively. Mean estimated g$_s$ for woody plants was 153, 135, and 131 mmol m$^{-2}$ s$^{-1}$ in wet/clay, dry/sand and dry/clay sites, respectively (S3 Fig). The coefficient of variation was 12% among the five dominant grass species and 29% among the 11 dominant woody species (S2 Fig). The larger variation among woody plants reflected large g$_s$ values for *Terminalia sericea* (258 mmol m$^{-2}$ s$^{-1}$) and *Ximenia caffra* (256 mmol m$^{-2}$ s$^{-1}$), which were found primarily in the wet/sand site (Table 2; S3 Fig).

**Discussion**

Results from this field-collected dataset highlight the importance of plant identity (functional type or species) and shallow soil moisture as primary drivers of g$_s$ in the tropical and sub-tropical savannas of Kruger National Park. Consistent with previous research, our analyses detected a negative g$_s$ response to VPD [49]. However, for several other meteorological variables, such as atmospheric CO$_2$ and shortwave radiation, the g$_s$ response found here was less consistent with previous research [7,50,51,52,53]. The data and model reported here, therefore, provide a perspective on site-scale values and drivers of g$_s$ that differs from many laboratory-based approaches and the difference appears likely to be driven by the over-riding importance of soil moisture on g$_s$ in these semi-arid ecosystems. While results differed from laboratory-based, leaf level measurements that emphasize the role of CO$_2$ and VPD, our results are consistent with canopy-level estimates of ET derived from a flux tower in Kruger Park [43].
Fig 3. Variable importance in random forest models of stomatal conductance for (a) grasses and (b) woody plants. For both grasses and woody plants shallow (0–20 cm) soil moisture and soil type (i.e., clay or sand) were the most and least important variables describing gs, respectively. Variable importance is the difference in prediction error before and after a predictor variable is randomly permuted. Large variable importance values indicate that specifying the variables incorrectly increases prediction error. See text for further variable descriptions.

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Fig 4. Partial dependence of grass and woody plant stomatal conductance ($g_s$) on environmental drivers. Values shown are predicted grass and woody plant $g_s$ as a function of each variable when all other variables are held at their mean value. Drivers listed in descending order of importance to grass $g_s$: shallow soil moisture (0–20 cm; a and b), vapor pressure deficit (VPD; c and d), atmospheric CO$_2$ (e and f), time of day (g and h), deep soil moisture (50–150 cm; i and j), wind speed (k and l), and shortwave radiation (m and n). Note that axis values are different for grasses and woody plants.

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Plant identity had the greatest effect on gs. In part, this reflected the fact that woody plant gs was twice as large as grass gs, although, even within grass and woody plant functional groups, species explained a large portion of variation in gs. Much of the ‘species’ effect was caused by large values for the woody plants Terminalia sericea and Xemenia caffra. Values for these two species were 79% greater than the mean gs for the other nine common woody species. The response of T. sericea, in particular, is not trivial because this species is common and often dominant in southern Africa and related species are common in Australia. Because much of the variation among species was caused by grasses vs. woody plants and 2 of the 11 woody species, it is possible that identifying and incorporating information on plant functional type and a small subset of species with large gs values may significantly improve regional models of gs [20,54,55].

Values of gs were surprisingly similar among sites. Mean gs values estimated across three growing seasons differed by only 3 to 26% among sites with the notable exception that woody gs values were 65 to 93% greater in the wet/sand than any other site. This reflected the dominance of the fast-transpiring T. sericea in the wet/sand site. In contrast, soil type had little effect on gs. This was surprising but likely occurred because our use of soil water potential values controlled for soil texture effects on soil water availability. Results suggested that gs is likely to be quite similar among a wide range of precipitation regimes and soil types, but that gs models that account for changes in species composition will produce better predictions than those that do not. It is important to note that if species or soil moisture data were not available, soil type would have been likely to help explain variance in gs, however, our results indicate that these ‘soil type’ effects are caused mostly by soil type effects on species composition and soil water availability.

After species and functional group, soil moisture was the most important driver of landscape-scale gs. It is important to note that soil moisture was estimated from measurements of soil water potential and not soil water content. Soil water potential measurements provide a better estimate of soil water availability than soil water content because soil water potential controls for the effects of soil texture. Shallow soil moisture (i.e., soil water potential in the 0–20 cm depths), in particular, was the most important driver of gs for both grasses and woody plants. Results indicated a fairly conservative stomatal control response with both grasses and woody plants decreasing gs roughly 50% between fairly moist water potentials of -0.1 to -0.5 MPa [29]. Midday leaf water potentials for grasses and woody plants at the Letaba study site have been reported to be roughly -2.5 MPa so stomatal control at water potentials of -0.1 to -0.5 MPa was surprising [30]. Our measurements of soil moisture were averaged across the 0–20 cm depths and across three hour time-steps. It is possible that our averaged, bulk soil measurements overestimated soil water availability in the rhizosphere (Fig 5)[56]. Regardless of the value at which stomatal control occurred, shallow soil water potentials were a dominant driver of both grass and woody plant gs during the six years of sampling in this study. Consistent with recent hydrologic tracer experiments in the park, these results suggest that both grasses and woody plants rely heavily on shallow soil water [30,33].

The dominant role of soil moisture appeared to affect the relationship between gs and other environmental parameters. For example, gs typically decreases with atmospheric CO₂ [19,21,57], yet, in this study gs increased with atmospheric CO₂. Atmospheric CO₂ was highest in the morning and decreased throughout the day [42]. Thus, atmospheric CO₂ decreased as soil moisture was likely to decrease (Figs 1 and 4) and shortwave radiation and VPD were likely to increase. Each of these diurnal parameter changes were likely to decrease gs at the same time that decreasing CO₂ concentrations were likely to increase gs. Because shallow soil moisture was a primary driver of gs, it is likely that soil moisture effects ‘masked’ CO₂ effects on gs. Diurnal variations in soil moisture of this type are common in semi-arid systems and
reflect the rapid midday exhaustion of rhizosphere water by root uptake and gradual replenishment of rhizosphere water through soil water flow and hydraulic redistribution [11,58,59].

Regardless of the mechanism, results suggest that CO$_2$ fertilization effects seen in some experiments may be difficult to observe in semi-arid savannas due to ‘masking’ effects of other drivers of plant growth such as soil moisture [18,60,61,62].

A similar result was found with shortwave radiation. Values of $g_s$ typically increase with radiation to a maximum $g_s$ threshold [5,52] but see [32]. Here, however, grass $g_s$ showed very little response to shortwave radiation and woody plant $g_s$ increased to and then decreased beyond shortwave radiation values of roughly 500 μmol m$^{-2}$ s$^{-1}$. It is possible that $g_s$ values in the field decreased as radiation increased because $g_s$ was primarily limited by soil moisture and plants were likely to exhaust soil water immediately around their roots in the morning, at the same time that radiation increased [46,50]. In short, it is likely that $g_s$ responses to radiation were precluded or ‘masked’ by $g_s$ responses to soil moisture. Such midday stomatal depressions are common [58].

Responses of $g_s$ to CO$_2$ and shortwave radiation highlight both the strengths and weaknesses of observational approaches. Data from this study provide estimates that account for the many interacting factors and emergent properties that affected $g_s$ during the years and conditions of this study. This approach showed, for example, the counter-intuitive positive response of $g_s$ to CO$_2$. The approach, however, is not well designed to isolate the individual effects of the drivers of $g_s$ because measurements were made in the field where multiple drivers change simultaneously. Results, therefore, are representative of $g_s$ values in field conditions.

![Soil water potential](https://doi.org/10.1371/journal.pone.0191396.g005)

**Fig 5.** An example of diurnal variation in soil water potential (MPa) at 20 cm over six days at the Letaba study site, 2010. Soil water potentials were greatest each day between 8 am and 11 am and smallest each day between 2 pm and 7 pm. Consistent with hydraulic redistribution, this indicated that shallow soils gradually became ‘wet’ each night and quickly dried between roughly 9 am and 5 pm.
but cannot provide strong inference to conditions unlike those observed during the study (i.e., extreme conditions associated with climate change).

In contrast to responses to shortwave radiation and CO₂, gs decreased with VPD as would be expected from laboratory-based studies. This effect was the second most important driver for grasses and also important for woody plants: gs decreased 29% and 21% with increasing VPD for grasses and woody plants, respectively. Our detection of a VPD effect was likely due, in part, to the fact that VPD and rhizosphere soil moisture are both likely to decrease gs through the day.

This study highlights the difficulties of modeling gs at the site- to landscape-scale [14]. Despite large sample sizes, the dataset was highly variable, and RF models explained only a modest proportion of variance, particularly for grasses. It is reasonable to expect that plant-to-plant variation would have explained a large portion of the variation in the dataset; however, averaging measurements over 2-hour increments (instead of 1-hour increments) provided nominal improvements in model power (i.e., 2% of error). This suggested that plant-to-plant variation explained little of the residual variance.

Variation in our dataset may have been accounted for by leaf-level environmental conditions. As stomatal aperture can change in response to leaf-level conditions, such as interstomatal CO₂, leaf water potential, and leaf temperature, including these leaf-level parameters may be necessary to explain much of the unexplained variance in the dataset [10]. Indeed, predictions from leaf-level models of gs that incorporate these types of parameters are often strongly correlated with observed values [8,10,12,63]. However, these studies tend to model variation in relatively small datasets, under fairly limited conditions and more importantly require detailed information on photosynthesis that are difficult to collect at large scales [7,10]. An important ‘next step’ for this research will be to compare the quality of model predictions developed here to model predictions from more commonly used semi-empirical models [7,10,64].

This study provides a prioritized list of variables important to landscape gs in this region. Results indicated that plant identity and shallow soil moisture are of greater importance than atmospheric conditions. While incorporating species into global circulation or land surface models may not be practical, it is possible to include plant functional type data or information on common species with very large gs values [64]. Species-level data is more likely to be useful for improving accuracy in canopy or ecosystem-level modeling [28]. This study also provides a model that can be used to produce continuous estimates of gs for the savannas of KNP using basic environmental data [30]. Such estimates are expected to improve evapotranspiration modeling for the savannas of KNP.

Finally, results provided novel insight into fundamental questions about savanna structure and function. The importance of shallow soil moisture to both grasses and woody plants was consistent with a rapidly-developing perspective of niche partitioning for soil water in savannas [30,33,65]. The importance of shallow water and the negative relationship between gs and CO₂ provided new support for the idea that CO₂ fertilization effects may be precluded by water limitation in semi-arid systems [60,61,62].

Supporting information

S1 Fig. Partial dependence of grass and woody plant stomatal conductance on soil type and precipitation regime.

S2 Fig. Modeled daily and seasonal gs for grasses and woody plants by study site.
S3 Fig. Mean daily stomatal conductance ($g_s$) for common grass and woody plant species estimated across three growing seasons, Kruger National Park, South Africa. (DOCX)

S1 Table. Studied species and their respective common names, families, and growth forms. (DOCX)

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