Drinking water intake of grazing steers: The role of environmental factors controlling canopy wetness

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ABSTRACT: Cattle obtain water primarily from the moisture in their feed and from drinking water. On pasture, the moisture content of the diet is influenced by plant tissue water (internal water) and surface moisture (external water), which may include dew, guttation, and intercepted rain, that influence the drinking water requirement. This study investigated the relationship between daily drinking water intake (DWI, L/d) of steers on pasture (19 steers with mean initial BW of approximately 400 kg) and soil and weather factors that are known to affect plant water status (dry matter content) and surface moisture formation and persistence. Daily records of weather conditions and DWI were obtained during 2 grazing seasons with contrasting spring, summer, and autumn rainfall patterns. Plant available water in the soil (PAW, mm) was modeled from actual and potential evapotranspiration and the water-holding capacity of the soil. The DWI averaged over the herd varied among days from 0 to 29 L/d (grazing season mean 9.8 L/d). The DWI on both dry (<0.2 mm rainfall on the corresponding and previous days) and wet (>2 mm) days increased with increasing temperature (mean, maximum, and minimum), sunshine hours, and global radiation and decreasing relative humidity, and the slopes and coefficients of determination were generally greater for wet days. Wind reduced DWI on wet days but had no effect on dry days. The DWI was reduced by up to 4.4 L/d on wet days compared to dry days, but DWI did not correlate with rainfall amount. Increasing PAW decreased DWI by up to >10 L/d on both dry and wet days. These results are all consistent with environmental effects on the water status (dry matter content) of pasture vegetation and canopy surface moisture, the associated effects on grazing-related water intake, and the corresponding balancing changes of DWI. Using the observed relationships with environmental factors, we derived a new model predicting DWI for any soil moisture condition, for both wet and dry days, which included mean ambient temperature and relative humidity and explained virtually all variation of DWI that was not caused by the random scatter among individual animals.

Keywords: model, natural pastures, precipitation, soil moisture, water intake

INTRODUCTION

Cattle on pasture satisfy their water demand primarily by drinking water and getting water from the moisture present in forage. Essentially, drinking serves to compensate for any lack of water in the forage to maintain a specific ratio of dry matter to water intake (Castle, 1972; Kume et al., 2010). This is particularly true for thermoneutral conditions (Khelil-Arfa et al., 2012), which are common for temperate climates. At pasture under temperate conditions, the intake of forage moisture can be large because of the low dry matter content of grazed forage (Castle, 1972). Large variability in daily drinking water intake (DWI) of cattle at pasture was strongly related to weather factors, such as temperature, humidity, wind speed, sunshine hours, evaporation, and rain (Castle, 1972; Castle and Watson, 1973; Ali et al., 1994). Although all these factors can affect the dry matter content of the grazed forage (Castle, 1972), they may also influence the surface wetness of the pasture canopy. It is a common phenomenon that plants in pastures are wetted by rain, dew (Janssen and Römer, 1991), and guttation (Meidner, 1977). These sources of dietary water have not generally or explicitly been considered as significant parameters of grazing-related water intake by cattle on pasture. Such information will be essential for grazing management (Bailey, 2004; Bailey,
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We performed a grazing experiment with steers over 2 yr with contrasting spring, summer, and autumn rainfall distributions. Daily records of weather conditions and DWI were obtained throughout both grazing seasons.

**Site Description**

The study was performed on a level area of permanent pasture at the Grünschwaige Grassland Research Station. It is located at the north end of the Munich Gravel Plain near Freising, Germany, at 435 m above sea level, latitude 48°23′N, and longitude 11°50′E (Schnyder et al., 2006). The pasture was dominated by grasses, of which *Lolium perenne*, *Poa pratensis*, and *Agrostis stolonifera* accounted for about 40%, 28%, and 9%, respectively, of the biomass. The pasture did not receive any fertilizer for at least 15 yr preceding the study, except for the excreta returned by grazing animals. The pasture offered abundant opportunities for shade: rows of >20-m-tall trees lined the western and eastern borders of the paddock, and another row of trees, oriented north–south, was situated in the middle of the paddock. Sward state was held constant by maintaining the compressed canopy height at 5 cm (SD of 0.9 cm). To this end the paddock was divided into a continuously grazed “core” area including the sole watering station and a temporarily grazed “buffer” area. The buffer area was added if actual sward height had fallen below target height, and part of the buffer area was fenced off when sward height exceeded the target height. Sward height was measured with a rising plate meter (Herbometre, Agro-Systèmes, La Membrolle-sur-Choisille, France) at about 120 to 150 locations 6 times per grazing season.

The climate is temperate humid with an annual mean air temperature of 9.0°C (SD of 0.8°C) and an annual precipitation of 775 mm (SD of 130 mm; Schnyder et al., 2006). All meteorological data were obtained from a German Weather Authority meteorological station (Munich airport; Table 1) located 3 km away.

**Grazing Experiment and Drinking Water Intake Measurement**

Measurements of grazing-related moisture intake are extremely time-consuming and potentially very imprecise because of large diurnal and day-to-day variations in grazing activity (Gary et al., 1970; Brown and Lynch, 1972; Kilgour, 2012), forage dry matter content (Jordan and Ritchie, 1971), and canopy wetness/surface moisture content (Burkhardt et al., 2009). Also, there is no universal and commonly accepted protocol for dew measurements (Richards, 2004). Moreover, the separate contributions of dewfall, dew rise, guttation, and intercepted water to leaf surface wetness and its intake are hardly distinguishable. We know of no attempt or reliable procedure to assess these sources of water intake in grazing studies. To avoid the technical issues, we took an indirect approach to assess the relationships between DWI and the weather and soil conditions known to affect leaf dry matter content and the formation and persistence of leaf surface moisture, including dew, guttation, and intercepted rain. During the entire grazing season (April to October) in 2010 and 2011, 10 and 9 steers (Limousin aged 16 mo, SD of 4 mo; initial BW of 411 kg, SD of 91 kg) were kept on the same pasture all day. Each animal had ad libitum access to a water bowl (SUEVIA HAIGES GmbH, Kirchheim am Neckar, Germany) and salt block to meet its requirements. No (semi)natural water bodies such as ponds or puddles provided water. The DWI was measured for each animal and each drinking bout. The water bowl was placed in a cage that allowed only 1 animal to drink each time, and the animal was identified by scanning its electronic ear tag (Texas Trading GmbH, Windach, Germany). It is unlikely that wildlife entered the cage because there were abundant water-bearing ditches in the vicinity of the pasture. The amount drunk was measured simultaneously by 2 independent systems. One system was a flowmeter (B.I.O-TECH e.K., Vilshofen, Germany; resolution of 0.1 kg) that

**Table 1. Mean monthly meteorological conditions at Grünschwaige Grassland Research Station during the grazing periods in 2010 and 2011:**

<table>
<thead>
<tr>
<th>Month</th>
<th>T&lt;sub&gt;mean&lt;/sub&gt; °C</th>
<th>RH, %</th>
<th>PET, mm/d</th>
<th>GR, kWh/m&lt;sup&gt;2&lt;/sup&gt;</th>
<th>Rain, mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>April</td>
<td>10.3</td>
<td>64.0</td>
<td>2.8</td>
<td>5.0</td>
<td>27</td>
</tr>
<tr>
<td>May</td>
<td>13.3</td>
<td>71.8</td>
<td>3.0</td>
<td>4.9</td>
<td>92</td>
</tr>
<tr>
<td>June</td>
<td>17.0</td>
<td>75.3</td>
<td>3.2</td>
<td>5.0</td>
<td>141</td>
</tr>
<tr>
<td>July</td>
<td>18.5</td>
<td>72.4</td>
<td>3.8</td>
<td>5.6</td>
<td>137</td>
</tr>
<tr>
<td>August</td>
<td>18.2</td>
<td>76.5</td>
<td>3.5</td>
<td>4.5</td>
<td>101</td>
</tr>
<tr>
<td>September</td>
<td>13.7</td>
<td>81.4</td>
<td>2.1</td>
<td>3.6</td>
<td>61</td>
</tr>
<tr>
<td>October</td>
<td>8.1</td>
<td>84.8</td>
<td>1.0</td>
<td>2.2</td>
<td>29</td>
</tr>
</tbody>
</table>
measured the amount of water flowing to the bowl as animals drank water. The other system was a weighing platform (Texas Trading GmbH) on which the animals stood during drinking. It measured the weight of the animal before and after each drinking event, the difference of which provided another measure for DWI. The animal code from electronic ear tags, the drinking duration, the amount of flowing water, and animal weight were recorded by a micrologger (PSION Industrial PLC, London, UK). The data were downloaded from the micrologger once a month, and the whole system was inspected for functionality. The weighing platform and the flowmeter produced similar data (Fig. 1), confirming their general reliability. However, the weighing platform had a lower resolution (1 kg) and fewer valid measurements ($n = 2,297$ compared to the flow meter with $n = 4,722$) because of the failure to determine the weight when animals moved on the platform. Hence, in the following analysis we only used the flowmeter data. Daily individual DWI was calculated as the sum of DWI for each drinking event for an individual steer, whereas daily mean DWI was obtained by dividing total daily water flow to the bowl by the number of animals in the herd.

**Capacity and Actual Level of Plant Available Water in the Pasture**

Monteith (1957) described 2 vapor sources for dew formation on a canopy: dewfall (a flux of vapor from the atmosphere) and distillation, or dew rise (a flux of vapor from the soil). Guttation means the exudation of water from hydathodes, xylem endings (specialized stomata) at the margins or tips of leaves (Meidner, 1977), and occurs when the rate of water supply from the roots is greater than the loss by transpiration (Hughes and Brimblecombe, 1994). Its amount is positively correlated with soil moisture (Hughes and Brimblecombe, 1994), as is dew formation from dew rise. Here we used plant available water (PAW) to represent the soil water status.

The average PAW capacity of the soil at our specific pasture was 135 mm, as estimated from rooting depth, soil texture, and organic matter content (Schneider et al., 2006). Lateral surface water flows were not expected because of the flat terrain. Hence, the level of PAW could be estimated for every day of the recording period on the basis of Allen et al. (1998), as shown by Schnyder et al. (2006), who quantified the effect of PAW on plant community $^{13}$C discrimination on all pastures of the Grünschaigie Grassland Research Station. Plant available water ($W_i$) was derived from the PAW of the previous day ($i-1$), rainfall ($R_i$), and actual evapotranspiration ($E_i$) of the corresponding day ($i$) as

$$E_i = E_{pot,i} \text{ for } P_{rel,i} = W_i/W_{capacity} \geq 0.3,$$

$$E_i = E_i \times W_i/(0.3W_{capacity}) \text{ otherwise},$$

where $E_{pot}$ is the potential evapotranspiration (mm), which was taken from the meteorological station. Calculation started after snowmelt (middle of March) when the soils were at PAW capacity. Here we defined a dry soil as a soil at PAW < 30% of the PAW capacity (45 mm in our case) because the plants then already reduce transpiration (Allen et al., 1998; see Eq. [2]) and a wet soil as a soil at PAW > 95% of the PAW capacity (130 mm in our case).

**Dry Days and Wet Days**

Rainfall occurred mainly at night (76% of all rainy days had rain between 1900 and 0700 h of the next day). As wetting by rain might affect the grazing-related water intake on the next day, we defined wet days as the days for which the total rain of the corresponding day and previous day was greater than 2 mm. Dry days were defined as days with less than 0.2 mm of rain. Days not classified into either category were termed null days.
RESULTS

Drinking Water Intake and Relation to Weather Variables

Over the 2 grazing seasons there was a greater number of wet days (n = 174) than dry days (n = 144), and 52 d were classified as null days. Data from 11 d were not included in the data set because of failure of the flow meter. The daily DWI averaged over the herd varied between 0 when none of the cattle drank any water and 29.4 L/d. Days without cattle drinking any water occurred either on wet days or on dry days with large PAW. The variation among individuals was even larger (range between 0 and 49.5 L/d), with individual drinking bouts of up to 29.4 L. On average, the SD among individuals within the herd for an individual day was 5.2 L/d (range of SD among days: 0 to 15.2 L/d), indicating considerable variation in the drinking behavior of individuals. There was, however, no evidence of a systematic deviation between animals. The SD among individuals meant that the daily mean DWI could only be determined with a 95% interval of confidence of 4.1 L/d. As a consequence, even a perfect model would not be able to predict the mean DWI on a particular day better than ±4.1 L/d within the total range of 0 and 29.4 L/d.

The mean DWI was highest on dry days (13.2 L/d), intermediate on null days (9.5 L/d), and least on wet days (7.1 L/d). It correlated significantly with all weather parameters, except for daily rainfall amount (for all categories of days) and wind speed on dry days (Fig. 2). Even within the category of wet days, the amount of rainfall had no influence on DWI. In general, correlations were highest for sunshine hours followed by global radiation, relative humidity, daily maximum ambient temperature, and daily mean ambient temperature. The strongest correlation between mean DWI and weather parameters was for wet days, followed by null days and dry days (see R² in Fig. 2). In general, null days were more similar to wet days than to dry days despite the small amount of rainfall that occurred on null days.

Drinking Water Intake under Dry Soil Conditions

Under dry soil conditions (PAW < 30% PAW capacity), DWI on wet days again correlated more closely with weather conditions than on dry days (Table 2), and in general, the correlations were closer than for the whole data set (compare Fig. 2 and Table 2). The daily mean ambient temperature correlated closely with DWI during dry days and wet days (Table 2), especially if a curvilinear relation was used (Fig. 3a) to account for the small influence of temperature below 10°C and the large influence above that temperature.

**Table 2.** Coefficient of determination ($R^2$) between weather variables and daily mean drinking water intake in dry soil conditions (PAW < 30% PAW capacity) on dry days (n = 24) and wet days (n = 17)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Minimum</th>
<th>Maximum</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry days</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean ambient temperature, °C</td>
<td>5.3</td>
<td>24.9</td>
<td>0.63***</td>
</tr>
<tr>
<td>Minimum ambient temperature, °C</td>
<td>1.2</td>
<td>15.1</td>
<td>0.57***</td>
</tr>
<tr>
<td>Maximum ambient temperature, °C</td>
<td>8.0</td>
<td>31.8</td>
<td>0.52***</td>
</tr>
<tr>
<td>Global radiation, kWh/m²</td>
<td>0.9</td>
<td>8.4</td>
<td>0.44***</td>
</tr>
<tr>
<td>Sunshine hours, h</td>
<td>0.0</td>
<td>15.4</td>
<td>0.36**</td>
</tr>
<tr>
<td>Relative humidity, %</td>
<td>42.5</td>
<td>99.2</td>
<td>0.32**</td>
</tr>
<tr>
<td>Wind speed, m/s</td>
<td>0.8</td>
<td>4.5</td>
<td>0.03</td>
</tr>
<tr>
<td>Wet days</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean ambient temperature, °C</td>
<td>8.5</td>
<td>25.3</td>
<td>0.78***</td>
</tr>
<tr>
<td>Minimum ambient temperature, °C</td>
<td>5.6</td>
<td>19</td>
<td>0.6***</td>
</tr>
<tr>
<td>Maximum ambient temperature, °C</td>
<td>10.8</td>
<td>32.4</td>
<td>0.64***</td>
</tr>
<tr>
<td>Global radiation, kWh/m²</td>
<td>1.2</td>
<td>8.0</td>
<td>0.45**</td>
</tr>
<tr>
<td>Sunshine hours, h</td>
<td>0.0</td>
<td>13.7</td>
<td>0.37*</td>
</tr>
<tr>
<td>Relative humidity, %</td>
<td>58.3</td>
<td>85.8</td>
<td>0.24*</td>
</tr>
<tr>
<td>Wind speed, m/s</td>
<td>1.0</td>
<td>5.7</td>
<td>0.2</td>
</tr>
</tbody>
</table>

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

At the same daily mean ambient temperature, the DWI was always lower on wet days than on dry days if the mean ambient temperature was less than 25°C (Fig. 3a). On hot days (mean ambient temperature > 25°C), rain had virtually no effect on DWI. The largest difference between dry and wet days of 4.4 L/d occurred at a mean ambient temperature of less than 10°C. Regressing DWI ($D$ in equations) and mean ambient temperature ($T_{\text{mean}}$) for the combination of dry days and a soil below 30% PAW capacity yielded ($R^2 = 0.7377***$, $n = 24$, *** indicates $P < 0.001$)

$$D_{\text{<30%,dry}} = 8.8 + 0.0011T_{\text{mean}}^3. [3a]$$

The same regression for wet days and a soil below 30% PAW capacity yielded ($R^2 = 0.8026***$, $n = 17$)

$$D_{\text{<30%,wet}} = 4.4 + 0.0013T_{\text{mean}}^3. [3b]$$

Drinking Water Intake under Wet Soil Conditions

Under wet soil conditions (PAW > 95% PAW capacity), which can supply sufficient soil vapor, it was assumed and evident (Fig. 3b) that rainfall would not increase leaf wetness above that already achieved by dew rise and guttation. Thus, for wet soil conditions, DWI on dry and wet days was described by a unique relation with the most predictive indicator, relative humidity, $H$ ($R^2 = 0.4985$, $P < 0.001$, $n = 41$):
Figure 2. Relation of daily drinking water intake averaged over the herd and weather variables and respective coefficient of determination ($R^2$) of linear regressions (solid lines) during dry days ($n = 144$), wet days ($n = 174$), and null days ($n = 52$). Dashed lines in the bottom panels indicate the averages of drinking water intake for each category. $T_{\text{min}}$ = daily minimum ambient temperature; $T_{\text{max}}$ = daily maximum ambient temperature; $T_{\text{mean}}$ = daily mean ambient temperature; SH = sunshine hours; RH = relative humidity; WS = wind speed; GR = global radiation. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. 
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The DWI decreased linearly with increasing relative humidity and reached zero at a relative humidity near 100%.

Relation between Soil Plant Available Water and Daily Drinking Water Intake

PAW covered a large range in both years, from 20 mm to the field capacity of 135 mm (Fig. 4). However, the 2 yr exhibited almost opposite seasonal patterns of PAW: in 2010 the soil was driest in the middle of the grazing season, whereas in 2011 soil PAW peaked in that period of the season. The fluctuations of DWI displayed an inverse pattern relative to PAW, especially in 2010. Even though the negative interaction was not evident for the 2011 grazing season as a whole, close inspection revealed that for shorter periods the DWI still correlated with PAW. For instance, PAW fluctuated frequently in the beginning of July in 2011, and each of these fluctuations was associated with an opposite variation of DWI.

The linear correlations between PAW and the different weather parameters were not significant (rainfall and minimum ambient temperature) or exhibited an $R^2 < 0.1$. The latter included mean and maximum ambient temperature, global radiation, humidity, and wind speed (data not shown).

In general, increasing PAW decreased DWI. The decrease of DWI was small until PAW exceeded about 70 mm and then became stronger (Fig. 5). This effect of PAW on DWI was particularly evident when mean ambient temperature exceeded 15°C. Again, the DWI on wet days was lower than that on dry days under similar weather conditions (mean ambient temperature either above or below 15°C).

Figure 3. Daily drinking water intake (DWI). (a) For dry soils (PAW < 30% PAW capacity) related to daily mean ambient temperature of dry days ($n = 24$) and wet days ($n = 17$). (b) For wet soils (PAW > 95% PAW capacity) related to relative humidity of dry days ($n = 5$) and wet days ($n = 36$).

$$D_{\text{dry}} = 0.0011 T_{\text{mean}}^3 + 8.8 + (-0.22 H + 22.1 - 0.0011 T_{\text{mean}}^3 - 8.8) \times (P_{\text{rel}})^4$$  \[5a\]

and

$$D_{\text{wet}} = 0.0013 T_{\text{mean}}^3 + 4.4 + (-0.22 H + 22.1 - 0.0013 T_{\text{mean}}^3 - 4.4) \times (P_{\text{rel}})^4.$$  \[5b\]

The measured and predicted DWI clustered along the 1:1 line (Fig. 6a) with RMSE of 4.2 and 3.6 L/d for dry and wet days, respectively. This uncertainty was similar to (or even smaller than) the average confidence interval of the DWI among individuals (4.1 L/d), indicating that practically all variation of the data was explained by the environmental variables included in Eq. [5a] and [5b].

Both Eq. [5a] and [5b] were also applied for null days. As expected, the model for dry days slightly overestimated DWI, and that for wet days slightly underestimated the DWI on null days (Fig. 6b), thus yielding slightly greater RMSE values of 4.3 and 4.1 L/d, respectively. Predicting the DWI for null days by using the average of the predictions for dry and wet days reduced the RMSE to 4.0 L/d, which was smaller than the RMSE of dry days even though the data for null days had not been used to develop the equations.

On average, DWI predicted for all days in the 2 grazing seasons with Eq. [5a] (applicable for dry days)
and Eq. [5b] (applicable for wet days) differed by 2.2 L/d, significantly less than the measured difference of DWI between dry and wet days (6.1 L/d). The average difference in DWI between dry days and wet days that received rainfall only at night was 2.7 L/d, but the difference became larger when rainfall occurred only in the morning. A further reduction of DWI was brought about by rainfall over a longer period of the day, especially when rainfall occurred throughout the day (night + morning + afternoon in Fig. 7).

**DISCUSSION**

This work reveals close relationships between DWI of steers grazing pasture and the weather and soil conditions that are known to affect plant water status and canopy wetness. This result is consistent with the working hypothesis that environmental factors enhancing forage-moisture intake during grazing lead to a reduced requirement for DWI and that such forage moisture includes both plant tissue internal water and also external water (i.e., dew, guttation, and intercepted rainwater). A positive correlation between DWI and the dry matter content of grazed forage was reported by Castle (1972); conversely, the same study also found negative relation-
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Figure 7. Daily drinking water intake (DWI) as affected by the diurnal timing and duration of rainfall events: dry days (n = 144) are days with no rainfall on the day corresponding to the DWI measurements and the previous day; night rain refers to rainfall only between 1900 h on the previous day and 0700 h on the corresponding day (n = 47). Morning is only from 0700 to 1300 h (n = 20), and afternoon is only from 1300 to 1900 h of the corresponding day (n = 11); nig+mor (n = 39) or nig+aft or nig+mor+aft mean that rainfall occurred at night and additionally in the morning (n = 24) or night and afternoon (n = 31) or night and morning and afternoon (n = 52). Error bars report the 95% confidence interval.

ships between DWI and rainfall and relative humidity. In water-constrained areas, grazing-related water is an important water source for herbivores. The grazing pattern would tend to maximize the benefit given by the greater water content of the pasture in the morning and evening to decrease the drinking water demand (Brown and Lynch, 1972; King, 1983). In the present work, the most striking effects on DWI resulted from (combinations or contrasts of) dry and wet soil conditions, rainfall events (yes or no), and the relative humidity of the air. Wet soils (high PAW) facilitate water uptake by plants and increase the relative water content (Volaire and Lelièvre, 2001), and they also promote guttation and dew formation via dew rise (Wilson et al., 1999). Rain wets the sward canopy, and high relative humidity enhances dewfall (Xiao et al., 2009) and slows the rate of evaporation of surface moisture from the canopy (Sentelhas et al., 2008). Explicit consideration of environmental factors affecting plant internal water content and canopy wetness led to a new model of the environmental controls on DWI of Limousin steers of specified age and live weight. The model was validated with null day data and also provided an acceptable fit (RMSE = 3.8 and 4.7 L/d for dry days and wet days, respectively) to DWI data obtained in a third year (2012; data not shown).

The model did not account for the possible effects of diet factors (e.g., dry matter intake, protein content, or salt consumption) and animal factors (e.g., sex, age, live weight, and performance) on DWI. Furthermore, it did not consider direct effects of environmental factors on total and related drinking water demand of cattle, as demonstrated and modeled by others (e.g., Winchester and Morris, 1956; Arias and Mader, 2011; Khelil-Arfa et al., 2012). Any variation of these factors would have affected the RMSE between modeled and measured DWI (which was ≤4.2 L/d, or ≤14% of maximum DWI) or influenced the modeled DWI via collinearities with those factors that were included in the model. All steers had ad libitum access to a salt block, ensuring that physiological requirements were satisfied. Compressed sward height was kept nearly constant by adjusting the grazing pressure. All animals were of the same breed and sex, had very similar ages and live weights, and exhibited no statistically significant differences in the relationship between live weight gain and DWI throughout the grazing seasons (data not shown). For these reasons, we suggest that diet (except for dry matter content) and animal factors had a relatively small effect on variation of DWI in this study. Nevertheless, there are several environmental factors, including temperature/exposure to solar radiation, relative humidity, and wind, that can exert an influence on the water demands of cattle (Marai and Haecb, 2010; Arias and Mader, 2011). The distinction between such direct effects on drinking water demand of animals and indirect effects, which act through variation of forage dry matter content and canopy surface moisture, is not trivial. This is complicated further by collinearities between weather factors (Arias and Mader, 2011). One approach to distinguishing the relative importance of such direct and indirect effects consists in comparisons of the present data with data from controlled environments or from studies conducted in pens/stables with diets of constant dry matter content and known amounts of drinking and total water consumption. Arias and Mader (2011) performed a comprehensive study of the effects of environmental variables on DWI in cattle finished in unshaded feedlot pens in several contrasting seasons, including summers and winters, in the humid continental climate of Norfolk, NE. Overall (winter plus summer), they found that minimum and mean ambient temperature and the temperature-humidity index (which were all collinearly related) were the most important predictors of water intake, whereas solar radiation, relative humidity, and wind speed had smaller (or nonsignificant) effects. As minimum temperature increased from 0°C to 20°C, DWI increased approximately 1.7-fold. Winchester and Morris (1956) reported on a controlled environment study with European cattle held at constant temperature and found a 1.5-fold increase in total water intake between 5°C at 25°C, whereas dry matter intake varied little
in the same temperature range. Brew et al. (2011) performed studies in thermoneutral conditions (5°C to 20°C) and found no effect of temperature on total water intake of 7- to 9-mo-old growing beef cattle housed in an open-sided barn. We estimate that for an increase of mean ambient temperature from 5°C to 25°C in conditions of dry days with dry soils, total water intake increased by 49% if we assumed a constant dry matter intake of 7.3 kg/d and a dry matter content of 0.22 kg/kg. This effect is very similar to that reported by Winchester and Morris (1956) and would suggest that the temperature effect on DWI on dry days with dry soils was essentially due to the temperature effect on total water demand of the steers. In comparison, DWI was much lower on wet days with dry soils when temperature was low, indicating a greater grazing-related water intake under these conditions. Indeed, cool conditions support a longer persistence of surface moisture on wet days (Dietz et al., 2007).

After accounting for ambient (minimum, mean, or maximum) temperature, other climatic factors generally contribute relatively little to the residual between modeled and observed DWI (Cardot et al., 2008). In hot and cold environments, however, the thermal balance of cattle, and hence water demand, can be affected quite significantly by air humidity, wind speed, and solar radiation (Blackshaw and Blackshaw, 1994; Berman, 2005; Mader et al., 2010). Given the ample opportunities for shade and wind shelter and the relative comfort range of daily mean ambient temperature (5°C to 25°C), however, the relevant heat stress and wind chill effects on water demand were probably quite small. On these grounds, we suggest that the observed variations of DWI, observed at a given ambient temperature (5°C to 25°C), however, the relevant heat stress and wind chill effects on water demand were probably quite small. On these grounds, we suggest that the observed variations of DWI, observed at a given ambient temperature, were mainly related to counterbalancing variations in grazing-related water intake.

The most convincing argument for strong variations in grazed forage water intake came from the observed relationship between DWI and PAW. Variations in PAW did not correlate, or correlated only marginally, with weather factors, meaning that weather effects on water demand and related effects on DWI must have been small. Increasing PAW decreased DWI up to >10 L/d on both dry and wet days. This effect was greatly enhanced by high atmospheric humidity and wet days. On wet days, the $R^2$ of each weather parameter with DWI was greater than on dry days, likely because of their effect on the formation or persistence of canopy surface moisture. The fact that rainfall in excess of 2 mm had no effect on DWI is related to the limited water storage capacity of the sward canopy. The absence of an effect of rainfall >2 mm on DWI is also supported by the raw data presented by Castle (1972). Wet days, high PAW, and high atmospheric humidity all promote and sustain high internal and external forage moisture contents (Wilson et al., 1999; Volaire and Lélièvre, 2001), which enhance the intake of forage water.

**Conclusions**

The present data and model strongly support the hypothesis that DWI of cattle grazing pasture is balanced by forage moisture intake, including internal plant tissue water and pasture canopy surface moisture, which includes dew, guttation, and intercepted rainwater. The originality of the model may be seen in the more mechanistic treatment of the environmental controls on DWI on temperate humid pastures.

**Implications**

Forage is an important source of water for grazers. A model of DWI of steers on pasture is presented that accounts specifically for the effects of environmental variables controlling forage moisture content. The model is driven by weather data and PAW in the soil. The approach used to derive the model may be used for further development of mechanistic DWI models that also account for animal physiology. Such tools will be essential for grazing management under future limited water resources, for understanding wildlife behavior, and for food authentication based on water isotopes.

**LITERATURE CITED**


Drinking water intake of cattle on pasture


