Seasonal changes in dendrometer-derived stem variation in apple trees grown in temperate climate**

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Abstract. Studies of daily changes in tree trunk diameter provide valuable information concerning growth patterns and their relationships with varying environmental conditions. To date, very few experiments with fruit trees evaluated the effects of climate variation on trunk shrinkage and the duration of the contraction and recovery phases and of growth. In this study, electronic dendrometers continuously monitored trunk diameter and trunk water storage dynamics of drip-irrigated ‘Gala’ apple trees (Malus x domestica Borkh.) during three growing seasons, which differed significantly in temperature, precipitation, air humidity and solar irradiation. It was found that trunk diameter and meteorological variables were closely related, even when excluding the effects of soil water limitations. During each growing season, the durations of the daily contraction phase began to increase with increasing water vapour partial pressure deficit, and decreased again in autumn, when vapour partial pressure decreased. Throughout the season, the duration of the growth phase tended to change inversely to that of both contraction and recovery phase. The relationship between maximum trunk shrinkage and vapour partial pressure was higher post than preharvest for all years studied. The duration of contraction, recovery, and growth phases may provide valuable information concerning seasonal changes and environmental drivers of water storage dynamics in apple trees.

Key words: maximum daily shrinkage, phase duration, contraction, recovery, stem radial increment

INTRODUCTION

Global climate change results in an increase in the intensity of solar radiation and higher air temperature, but also decreases precipitation during the growth season in temperate climates (IPCC, 2021). These conditions will increasingly impede crop production, as already observed in various fruit growing regions worldwide. These changes will reduce soil water availability, decrease air humidity, and intensify the environmental stresses for crop plants. For environmental studies, rapid and cost-effective sensing techniques for monitoring the response of fruit trees to climatic stresses will be essential.

Optimised irrigation management will become important for the management of crop production (Olesen et al., 2011), and drip irrigation is commonly used in tree fruit production to minimize effects of potential droughts, even in temperate climates. Automated dendrometers can continuously monitor the trunk diameter of trees to analyse tree responses to soil and environmental conditions (Deslauriers et al., 2003; Drew et al., 2008; Irvine and Grace, 1997). Analysing the daily and seasonal variations in trunk size provides valuable real-time information for the irrigation management of fruit trees (Cohen et al., 2001; Intrigliolo and Castel, 2007; Ortuno et al., 2006; De Swaef et al., 2014).

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The daily variation in tree stem diameter results from both irreversible growth and reversible trunk shrinkage and swelling associated with the plant water balance (Deslauriers et al., 2007b; Irvine and Grace, 1997; McLaughlin et al., 2003). In general, daytime transpirational water losses partially empty the wood water storage and result in reversible trunk shrinkage (Devine and Harrington, 2011). Thus, the extent of daytime shrinkage (contraction) depends on both the actual water vapour partial pressure deficit (VPD) of the air and soil water availability, i.e., precipitation and/or irrigation. The contraction of the trunk during the day is usually reversed at night. Reduced VPD due to lower night temperatures, concomitant with darkness-induced stomatal closure, largely decreases transpiration, inverts water radial flows and facilitates rehydration and replenishment of plant water reserves due to soil water uptake (Belien et al., 2014; Steppe et al., 2006; Vieira et al., 2013; Zweifel et al., 2006). Radial trunk growth and wood formation take place in parallel, which continuously and irreversibly increase the trunk diameter (Oberhuber et al., 2014). Therefore, analyses of the daily dynamics of trunk diameter throughout the year also provide quantitative information concerning tree growth patterns as they are affected by both short-term and long-term environmental conditions such as VPD, soil and air temperature, soil water content, and precipitation. Many studies on forest and fruit trees such as peach, plum, olive, and apple highlighted this relationship in the boreal zone, and in temperate and Mediterranean climates (Cohen et al., 2001; Urrutia-Jalabert et al., 2015; Zweifel et al., 2006).

From the diurnal water movement, it is obvious that the maximum daily shrinkage (MDS) of the trunk sensitively reflects the responses of fruit trees to soil water availability and plant water deficit stress. Indeed, this index has been applied to evaluate long-term changes in plant water status of plum and citrus trees (Intrigliolo and Castel 2006a; Intrigliolo and Castel, 2006b; Ortuno et al., 2010). Other studies highlighted the close relationships between the seasonal variation in MDS and the relevant environmental factors in plum and apple trees (Du et al., 2017; Fernández and Cuevas, 2010; Kalaj et al., 2018; Liu et al., 2011; Ortuno et al., 2010; Chitu and Paltineanu, 2019; Paltineanu et al., 2020). Strong correlations between MDS and stem water potential were reported for citrus (Ortuno et al., 2004), peach (Marsal, 2012), plum (Intrigliolo and Castel, 2006a), almond (Goldhamer and Fereres, 2001), pomegranate (Galingo et al., 2014), persimmon (Badal, 2010), apple (Li et al., 2011), citrus (García-Tejero et al., 2012; Ortuno et al., 2006) and cherry trees (Abdelfatah et al., 2013; Blanco et al., 2018).

For forest trees, more detailed temporal analyses of daily trunk diameter changes were performed. Diel variations in this parameter can generally be divided into three distinct phases (Herzog et al., 1995), 1) contraction, 2) expansion and 3) increment phase (Deslauriers et al., 2007b; Downes et al., 1999; Giovannelli et al., 2007; Hu and Fan, 2016).
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radiation on MDS and SRI, and also assessed the interaction of climatic factors and the duration of the different phases for both pre- and postharvest periods in each year.

MATERIAL AND METHODS

During the growing seasons of 2018, 2019 and 2021, the study was performed on ‘Gala’ apple trees (*Malus domestica* Borkh.) on M9 rootstock in the experimental orchard of the Leibniz Institute for Agricultural Engineering and Bioeconomy (ATB) located in Marquardt, Germany (52°28’2” N, 12°57’39’’ E) in the vicinity of Potsdam. The trees, which were trained as tall slender spindles with a 3.5 m maximum height, were planted with 4 m between each row and a 1 m in-row spacing. Trees were trickle irrigated (dripper distance: 50 cm, flow rates: 1.5 ± 0.1 L h⁻¹, two drippers each tree) three times a week irrespective of weather conditions from April to October.

Generally, the soil type is a loamy sand with low water-holding (field capacity: 26.5 ± 0.7% vol) and cation-exchange capacity; only the topsoil is predominantly silty sand (sands: 71-88%, silt: 8-15%, clay: 4-14%, Corganic: 0.4-1.7%, soil number: 0-34; pH: 6.6-8.4). In the experimental area, soil cover showed small-scale variations due to the glacial and post-glacial origin of the parent material (ATB, 2021; Trost, 2021). The average annual temperature and rainfall were 8.7°C and 590 mm, respectively, over a period of 30 years.

Within the orchard, a weather station automatically recorded air temperature (°C), relative air humidity (%), global normal irradiance (GNI; W m⁻²) and precipitation (mm) every minute and stored the averages every hour. Daily means and the means corrected for the day length were analysed. The water vapour partial pressure deficit (VPD, kPa MPa⁻¹) was calculated from the difference between the actual and the saturation water vapour partial pressure of the air divided by the total air pressure (von Willert *et al*., 1995).

From the end of May, i.e., the cell division phase of fruit until a few weeks after harvest, trunk diameter variations were measured using DD-L dendrometers (Ecomatic GmbH, Dachau, Germany), installed 70 cm above ground, approx. 50 cm above the grafting zone. Data were recorded at 1-min-intervals with a CR10X data logger with an AM416 multiplexer (Campbell Scientific, Logan, USA) and means were automatically stored every 15 min.

Time series of diel trunk diameter cycles were processed separately for each of six randomly selected trees and the duration of the three distinct phases of each circadian cycle was extracted (Fig. 1). The contraction phase (1) was identified as the period between the maximum daily diameter during the morning and its minimum in the subsequent afternoon. The expansion (recovery) phase (2) denotes the time from this minimum to the maximum of the previous day. The trunk increment phase (3) relates to the time necessary for the “stem radial increment” (SRI), i.e., the low portion of overall radial trunk growth. The maximum daily shrinkage (MDS) was calculated as the difference between the maximum and minimum trunk diameter.

All trunk diameter parameters were averaged over all trees monitored. Calculations were performed using Excel 2016 (Microsoft, Redmond, USA). Raw data were pre-processed using the SUMPRODUCT function (window size = 7), based on the Savitzky-Golay smoothing algorithm (Savitzky and Golay, 1964). Regression and Pearson correlation coefficients were then calculated using IBM SPSS 22.0 for Windows (IBM, Armonk, USA) to analyse the significance (p < 0.05) of the effects of climatic factors on each relevant parameter for each year.

RESULTS AND DISCUSSION

The conditions during 2018 and 2019 were much hotter and drier than in 2021 (Fig. 2A), with warmest temperatures being measured in June and July; similarly, transpiration demands (VPD) and total daily global normal irradiance (GNI) were also higher in those years (Fig. 2B).

As a result (Table 1), the general climatic conditions ranged from the extremely dry, hot and sunny summer period in the growing season of 2018 (Herppich *et al*., 2020), to the hot and semi-dry season in 2019 to the moderately hot and humid season in 2021. Precipitation typically occurred in April, August and September for all of those years (Fig. 3).

The typical circadian variations in trunk diameter, recorded by dendrometers, with a maximum diameter in the early morning and a minimum in the afternoon (Fig. 1), are known to reflect diel radial water flows (Downes *et al*., 2018).

Fig. 2. Sum of average $T_{air}$ (A) and the global radiation (B) of apple trees during the growing seasons of 2018, 2019 and 2021.
1999). Generally, the reversible diurnal variation of the stem radius is driven by transpiration and soil water supply. In fact, during daytime, when transpirational water loss often exceeds soil water uptake, the stored water in the vessels is depleted (Zweifel and Häsl, 2001). However, water storage will be recharged again from soil water during the night (Scholz et al., 2008), when transpiration is low due to reduced VPD (von Willert et al., 1995). The overall seasonal variations in these general patterns, as indicated by the maximum daily stem shrinkage (MDS), were similar for the three years of the experiment although amplitude and time frame differed (Fig. 3). In late April (2018) and Mid-May (2019 and 2021), MDS began to increase, reaching maximum values of 600 µm (2018), 260 µm (2019) and 450 µm (2021) in May-July, June-July and June, respectively. During late August, MDS was still high (500 µm) in 2018 but much lower at 150-200 µm in both 2019 and 2021. After harvest and, more prominently, after early autumn rains, MDS dropped slightly in 2018 and 2019 to values of approx. 100 µm (2018) and 50 µm (2019 and 2021; Fig. 3). In late October 2018, MDS was still high at 70 µm but gradually decreased to 20 µm in the other two years.

The day-to-day variation in the MDS in trees for all of the years monitored were closely related to climatic factors, especially to VPD and soil water availability. This finding confirms those of earlier studies reporting that MDS is highly affected by climatic conditions (Conejero et al., 2007; Fereres and Goldhamer, 2003; Kalaj et al., 2018; Ortuno et al., 2006). Both MDS and VPD were found to be higher, and precipitation lower in 2018 than in 2019 and 2021 (Table 1, Fig. 3). However, because VPD denotes the true force required to physically drive transpiration (von Willert et al., 1995) and thus, plant water loss, the amount of water that the trees lost to the atmosphere was higher in 2018 than in the two other years. In addition, prolonged periods of drought due to the sporadic and sparse rainfalls in 2018 quite often prevented the replenishment of daytime water loss from the soil water, despite the application of regular drip irrigation. Consequently, trunk water storage was highly depleted and MDS became extremely high in this year. By contrast, in the other two years precipitation was more frequent and also its magnitude was much larger. In this context, Herppich et al. (1994) showed that even minor rain events, accompanied by reduced VPD, much more effectively improved plant water status than regular irrigation under otherwise dry conditions.

In both 2018 and 2019, the stem radial increment (SRI) started in early-April, reaching its maximum (≥ 50 µm d⁻¹) at the end of April to early May and decreased again to 20 µm d⁻¹ at the end of June with the beginning of summer.

### Table 1. Major climate parameters recorded during the main growing periods (Mid-April to Mid-October)

<table>
<thead>
<tr>
<th>Year</th>
<th>minT range (°C)</th>
<th>maxT_air (°C)</th>
<th>minT_air (°C)</th>
<th>maxVPD (kPa MPa⁻¹)</th>
<th>dailyGNI (W m⁻²)</th>
<th>sumRain (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2018</td>
<td>14.0 – 23.3</td>
<td>30.0</td>
<td>1.7</td>
<td>30.8</td>
<td>302</td>
<td>117</td>
</tr>
<tr>
<td>2019</td>
<td>11.7 – 23.1</td>
<td>29.4</td>
<td>1.8</td>
<td>29.7</td>
<td>293</td>
<td>258</td>
</tr>
<tr>
<td>2021</td>
<td>7.0 – 21.7</td>
<td>29.0</td>
<td>1.5</td>
<td>29.9</td>
<td>293</td>
<td>370</td>
</tr>
</tbody>
</table>

Given are monthly air temperature ranges (minT, °C), maximum daily T_air (maxT_air), minimum daily T_air (minT_air), maximum water vapour partial pressure deficit (maxVPD, kPa MPa⁻¹), the total daily global normal irradiance (dailyGNI) and total rainfall per growing season (sumRain, mm).

![Fig. 3. Maximum daily shrinkage (MDS; black solid line), daily mean vapour pressure deficit (VPD; red dotted line) and daily precipitation (blue vertical column) during 2018 (A), 2019 (B) and 2021 (C). Harvest days (harvest time) are indicated for each year.](image-url)
During the remaining months of the growth season, SRI was low and ranged between 20 and 0 µm d⁻¹ (Fig. 4A). These patterns varied slightly between the years that were monitored, but in 2021, SRI started to increase and obtained its maximum value with one month delay.

SRI is related to changes in the trunk diameter (Deslauriers et al., 2003); thus, its overall sum closely reflects trunk growth (Fig. 4B). Hot and dry climatic conditions in 2018 decreased tree growth. Water deficit stress is known to limit SRI, however, because the trees were regularly irrigated throughout the growing seasons, soil water availability may be excluded as the primary negative parameter. This was particularly the case in 2018, when elevated temperature and high VPD impeded stomatal conductance and photosynthesis thus reducing carbon yields (Herppich et al., 2020). In 2021, climatic conditions not only delayed the start of but also limited growth during the summer. Nevertheless, other factors such as the phenological stage of the trees and crop load also have a potent effect on trunk growth independently of tree and soil water status (Berman and Dejong, 2003). In trees, crop load may compete for assimilates and hence, reduce the availability of carbohydrates for trunk growth (Intrigliolo and Castel, 2007).

The correlations of MDS and air temperature, global radiation, VPD and precipitation were significant with the exception of precipitation in 2018 and 2019 (Fig. 5). In pooling the respective data for the three years that were monitored, the coefficient of determination ranked the parameters as VPD > temperature > global radiation > precipitation. These results were expected, because both increasing VPD and decreasing soil water availability increase the soil-to-leaf water potential gradient (Drew et al., 2008; Steppe et al., 2006) and, consequently, the MDS of the fruit trees closely reflects the water status of the plant (Conejero et al. 2007; Liu et al., 2011; Ortuno et al., 2010). High relative humidity, i.e., low VPD decreases transpirational water loss and, thus, not only reduces the depletion of water storage but potentially facilitates replenishment (Köcher et al., 2012; Scholz et al., 2007). By contrast, warm and dry days with high VPD increased transpiration and the use of stored water and also increased trunk shrinkage (Steppe et al., 2006; Zweifel et al., 2005).

Statistical analyses did not reveal a correlation between SRI and the climate factors monitored in all years of this study. By contrast, a close relationship between air humidity and rainfall with SRI was found in rain-fed
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forest trees (Deslauriers et al., 2007a; Urrutia-Jalabert et al., 2015; Vieira et al., 2013). In the present study, this discrepancy appears to be reasonable however, because the trees were regularly irrigated and less drought stress occurred, thereby resulting in the dominant effects of high VPD and temperature on tree growth.

In the present study, the duration of the contraction phase increased in early to late May, continuing until mid to late August and then decreased to reach a minimum in late September (Fig. 6A). This seasonal pattern reflects the results published for various forest trees (Drew et al., 2008; Vieira et al., 2013) indicating longer trunk contraction phases during the summer than in other seasons. Transpiration and the concomitant radial movement of water out of the water-storing wood governed the extent of tree trunk contraction and the duration of this phase (Deslauriers et al., 2007a; Steppe et al., 2006). VPD and soil water deficit, which are both high during dry and hot summers, control these water flows.

Furthermore, the duration of the recovery was generally longer than that of the contraction phase in the present study (Table 2), showing maxima between June and August when day length is longest, and slightly decreased values from late-September to early-October (Fig. 6B). This seemed to be the overall trend. However, Vieira et al. (2013) also reported that recovery phases were longer than both contraction and increment phases in early-summer and summer (Vieira et al., 2013). In addition, previous studies indicated that enhanced temperature and day length increased the duration of the recovery phases following higher transpirational water losses (Čermák et al., 2007). In general, the duration of the recovery peaked when the total sap flow was highest (Deslauriers et al., 2007a) due to the correlations of both variables with transpiration rates.

The duration of SRI (Fig. 6C) was negatively correlated with that of both the contraction and the recovery phases during the early growing season (April to May); the duration of SRI decreased to its minimum during summer (June to August). In summer, the inverse relationship between the duration of recovery and SRI phases may be due to the fact that a longer recovery phase, i.e., the replenishment of the water storage, means less time and less water for growth (Drew et al., 2008). As a general seasonal trend, the duration of SRI decreased during winter, reaching its minimum in early summer and increased again during late summer and autumn (Vieira et al., 2013). Furthermore, sap flow and tree transpiration typically correlate negatively with both the amplitude and the duration of SRI (Deslauriers et al., 2007a).

Single factor correlation analyses (from April to October) highlighted that the duration of contraction phases (Fig. 7A) positively correlated with the daily means of VPD ($r \geq 0.56$, $p < 0.001$), $T_{air}$ ($r \geq 0.55$, $p < 0.001$) and the global normal irradiance (GNI; ($r \geq 0.48$, $p < 0.001$) for all years. Thus, this confirmed the similar findings of Drew et al. (2008) who reported a positive correlation between the monthly mean duration of the contraction phases and the monthly means of global irradiance. Furthermore, the relation between $T_{air}$ and the duration of

<table>
<thead>
<tr>
<th>Year</th>
<th>Contraction (max / min, h)</th>
<th>Recovery (max / min, h)</th>
<th>SRI (max / min, h)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2018</td>
<td>8.3 / 8.0</td>
<td>12.3 / 11.1</td>
<td>4.0 / 2.0</td>
</tr>
<tr>
<td>2019</td>
<td>8.0 / 7.0</td>
<td>11.0 / 10.7</td>
<td>7.0 / 3.5</td>
</tr>
<tr>
<td>2021</td>
<td>6.0 / 6.3</td>
<td>11.9 / 10.7</td>
<td>8.3 / 4.3</td>
</tr>
</tbody>
</table>

Fig. 6. Time series of the duration of contraction (A), recovery (B) and radial stem increment (SRI; C) during the growing periods of 2018 (red line), 2019 (green line) and 2021 (blue line). Picking dates are indicated for each year.

Table 2. Overall range of the seasonally maximum and the minimum duration of the contraction, recovery and growth (SRI) phases in the three years of investigation.
the contraction phase is known to depend on the respective season and may be negative in autumn but positive in winter (Vieira et al., 2013).

It is interesting to note that no correlation was found between the duration of the contraction phase and precipitation in the dry (and hot) years of 2018 and 2019 ($r = 0.16$, Fig. 5A), whereas a significant relationship was found in the wet (and cool) year of 2021 ($r = 0.26$, 0.005). This agrees with the findings of Deslauriers et al. (2007a) and Vieira et al. (2013), who assumed that the number and the duration of rain events did not affect the contraction phase. With the exception of precipitation, the correlation coefficients in 2019 and 2021 were higher than in 2018, ranking in the order VPD $>$ $T_{air}$ $>$ $GNI$ $>$ precipitation. In general, the link between the duration of contraction and the climate variables was less clear than that of its amplitude, i.e., of MDS (Vieira et al., 2013).

The contraction and recovery phases varied in response to climate in the present study, thereby highlighting the close relationship between these phases (Fig. 7B). The relationship between climate factors and the duration of the recovery phase was, however, weaker than that of contraction. During the growing season, $T_{air}$ ($r \geq 0.39$, $p < 0.001$) and VPD ($r \geq 0.20$, $p < 0.001$) correlated positively with the duration of recovery but negatively with precipitation ($r = 0.20$, $p < 0.005$; only for 2021) whereas no correlation was apparent between the duration of recovery and $GNI$ (Fig. 7B). Vieira et al. (2013) also reported a high positive relationship between the air temperature and the duration of recovery in the summer. The strength of the correlation between the duration of the recovery phase and the climate parameters varied widely between the various years studied.
The duration of the increment phase (Fig. 7C) was negatively correlated with $T_{air}$ ($r = 0.59$, $p < 0.001$), VPD ($r = 0.44$, $p < 0.001$) and GNI ($r = 0.32$, $p < 0.001$). As also reported earlier, the duration of the increment phase was negatively correlated with minimum daily $T_{air}$ in non-irrigated trees (Drew et al., 2008), while Vieira et al. (2013) indicated a high positive correlation between the maximum $T_{air}$ and the duration of this phase in early summer.

High intensity of solar radiation generally increases leaf temperature and, thus, the VPD between the leaf and the air (von Willert et al., 1995). This, in turn, increases transpiration and water losses of the tree, thereby reducing its tissue turgor and, consequently, cell enlargement and growth (Fritts, 1958). Therefore, a high GNI in summer may thus impair the conditions favourable for growth and limit SRI (Urrutia-Jalabert et al., 2015).

As expected for irrigated trees, the duration of SRI was also weakly but positively correlated with precipitation in the present study (Fig. 7C). Nevertheless, the effects of precipitation and the duration of the increment phase closely depends on the respective season, with negative correlations in summer but positive ones occurring in autumn (Vieira et al., 2013).

The coefficients of determination for the relationships between VPD and MDS, the duration of the phases of contraction, recovery and SRI are shown for pre- and postharvest periods (Fig. 8). The relationship between MDS and VPD was higher for post-rather than preharvest stage in all years (Fig. 8A). However, the relationships between the duration of the different phases and VPD were not markedly different at the pre- and postharvest stage (Fig. 8).

![Fig. 8. Scatter plot between water vapour partial pressure deficit (VPD) and maximum daily trunk shrinkage, MDS (A), durations of contraction (B), recovery (C) and stem radial increment, SRI (D) during preharvest (black circle) and postharvest (red triangle) period of three years.](image)
In all of the years studied, duration and amplitude (i.e., MDS) of the contraction phases were closely and positive correlated; however, this relationship was better before rather than after harvest (Fig. 9). As expected, the amplitudes of both contraction and increment also depended closely on the duration of the respective phase (Deslauriers et al., 2007a; Drew et al., 2008a). Given that both components (amplitude and duration) are interdependent, the climatic or physiological factors acting on one must also influence the other (Deslauriers et al., 2007a), as reported for contraction in forest trees during the late summer and autumn (Vieira et al., 2013) and for recovery and increment in early summer. For modelling water storage dynamics, parameters such as leaf area, root area, and crop load could be considered.

CONCLUSIONS

1. Meteorological parameters such as vapour partial pressure, air temperature or total daily global normal irradiance significantly affect the variation in the trunk diameter of irrigated apple trees as indicated by maximum daily shrinkage.

2. The maximum daily shrinkage of apple trees highly depends on both the daily and seasonal variations in these climatic factors.

3. The duration of the three characteristic phases of the differences in trunk diameter were related to these factors during the entire growing season.

4. Evaluation of the duration of the distinct daily phase (especially that of contraction and stem radial increment) and their variation with climate and tree growth stages provide information concerning the environmental drivers of stem water storage-dynamics in apple trees.

5. The seasonal variation in the effects of crop load, leaf area, and leaf area to fruit and leaf area to wood ratios on the duration of the three phases of trunk diameter changes and their interactive relationships with the environmental parameters should be explored further.

Conflict of interest: The authors declare no conflict of interest.

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Fig. 9. Scatter plot between the daily amplitude of maximum daily shrinkage (MDS) and the duration of contraction during the growing period of 2018 (A), 2019 (B) and 2021 (C).


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