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**Original Research Paper**

# Modelling Canopy Stomatal Conductance of *Hedysarum scoparium* and Long-term Prediction in Semiarid Region in China

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## ABSTRACT

*Hedysarum scoparium* (*H. scoparium*) is a fast-growing and drought-resistant shrub species that has been extensively used for grassland restoration and agricultural landscapes protection such as farmland protection and wind shelterbelts in semiarid regions of Northwestern China. To date knowledge about the water consumption characteristics and physiological response to environmental factors of *H. scoparium* is quite limited. Thus, the primary objective of this study was to create a Jarvis-type model of canopy stomatal conductance ($g_s$) in *H. scoparium* shrubs and use the model to predict long-term trend variations. During the research, the sap flow rate ($J_S$) of four shrubs with diameters of 29, 21, 15, and 11 mm was monitored under natural conditions. Meteorological factors were obtained at a flux tower on site. Results indicate that the meteorological variables are significantly correlated with $g_s$, which increases exponentially with the increase in vapour pressure deficit (VPD) after controlling for the additional effects of air temperature ($T_a$) and solar radiation ($R_n$). The Jarvis model was set up to express the variation observed in $g_s$, and the sequence affecting the accuracy of the model is $R_n$ > VPD > $T_a$. This study attempts to probe $g_s$ of *H. scoparium* by using $J_S$ and applying Jarvis-type model, the proposed Jarvis-type model offers a solution to the above-specified problems, which also solves the time lag issue in $g_s$ prediction. The conclusions obtained in the study can provide the intentionality reference and conservation management guidance for environment protection and desertification combating.

## INTRODUCTION

*Hedysarum scoparium* (Fisch. & C.A. May) (*H. scoparium*) is a vivacious leguminous subshrub mostly distributed in the arid and semiarid regions of China. The extensive root system of the large shrub (the maximum height reaches 3.0 m) can spread up to 10 m horizontally and penetrate up to 8 m deep into the soil. The intensive root system allows *H. scoparium* to survive desert sandy soil and tolerate extreme dry climate which also makes *H. scoparium* an ideal xerophyte shrub to fight against desertification in semiarid areas of China (Deng et al. 2015). Thus, its ecological and environmental benefits are more obvious.

China is known as a country that is severely affected by desertification. Thus, many ecological engineering projects such as “Three-north Forest Protection Project” have been established in the past decades to deal with this problem. Many studies have already proven that the restoration of desert ecosystems using xerophyte shrubs produces a wide range of hydrological effects (Wang et al. 2012). These findings are more applicable to semiarid regions because of the spatial variability in meteorological factors, particularly rainfall. However, knowledge about the water requirements, transpiration characteristics and physiological response to environmental factors of these desert-living shrubs such as *H. scoparium* is limited; thus, a better understanding of transpiration by desert plants is strongly needed (Deng et al. 2015). Moreover, studying the dynamic prediction model of plant transpiration and obtaining the dynamic stomatal change are critical to the goal of afforestation and soil erosion prevention by using *H. scoparium* plantation.

For decades, various methods have been used to measure plant transpiration (Dzikiti et al. 2007). Among these measurement techniques, stem heat balance (SHB) has been widely applied in transpiration studies because of its advantages of accuracy, continuous automatic monitoring, avoidance of certain sample wood damages, and ease of use in the field (Kigalu 2007, McDowell et al. 2008, Stephen et al. 2008). In addition, because of long periods of time monitoring the sap flow ($J_S$), an accurate measurement of $J_S$ and the inversion of the Penman-Monteith (PM) equation allow estimates of canopy stomatal conductance ($g_s$) response to environmental variables to be tested on a daily and a seasonal bases (Kigalu 2007, McDowell et al. 2008).

Transpiration ecohydrological research indicates that plants regulate $J_S$ via changes in $g_s$ in response to variations in environmental variables (Xia et al. 2008, Yue et al. 2008). However, the interaction between $g_s$ of *H. scoparium* and these variables is still unclear. To date, many models such as Ball-Berry and Leuning models have been established to predict $g_s$. But a wide range of model types indicate that there is an incomplete knowledge of interactions among meteorological variables. Thus, during this research, we choose Jarvis-type model for its accountability, utility and manipuility (Deng et al. 2015).

The objectives of this study are to estimate the $g_s$ from $J_S$ measurements (by using SHB method) by inverting the PM equation and to set up an empirical Jarvis-type model to predict $g_s$ changes induced by the environment. Our results will provide the information required to support the management of this ecologically important plant in semiarid northwestern China.

## MATERIALS AND METHODS

**Study area:** The research station is located in Yanchi County, Ningxia autonomous region (longitude of 106°3002, latitude of 37°042; altitude of 1,354 m) (Fig. 1). The annual precipitation averages 287 mm. The mean annual potential evaporation is 1,273 mm. The mean annual temperature of approximately 8.1°C. The wind speed ($W_S$) averages 2.6 m.s$^{-1}$. The landscape is a typical transitional zone whose terrain changes from the Loess Plateau to the Ordos Plateau. The soil types are primarily dark loessial soil and eolian sandy soil. The vegetation type varies from dry steppe species to desert grassland (Deng et al. 2015).

**Sap flow and meteorological measurements:** Model SGB9, 13, 16 and 25 gauges (Flow32 meters, Dynamax Inc., Houston, TX, USA) were attached to the stems of 17-year-old *H. scoparium* with stem diameters of 29, 21, 15 and 11 mm. The theory and methodology of using $J_S$ gauges are described in detail by Deng et al (Deng et al. 2015).

Meteorological data were obtained using an on-site flux tower. The unit contains one CNR4 net radiation sensor, one CMP3 total radiation sensor, one HMP155a, one 034B anemometer, two ombrometer sensors and six SI-111 infrared temperature sensors that measured $R_n$, net radiation, RH, $W_S$, rainfall (P), and $T_a$, respectively (Deng et al. 2015).

**Modelling stomatal conductance:** In our research, we calculate the $g_s$ using an improved PM equation (Deng et al. 2015).

$$g_c = \frac{\gamma \lambda E_c g_a}{\Delta R_n + \rho C_p VPD g_a - \lambda(\Delta + \gamma) / E_c} \qquad ...(1)$$

Where $R_S$ is shortwave radiation (W.m$^{-2}$), $R_n$=0.8 $R_S$, ë is latent heat of moisture evaporation (2465 J.g$^{-1}$), $r_a$ is the leaf boundary layer resistance (s.m$^{-1}$), $g_a$ is the aerodynamics conduction degree (m.s$^{-1}$), $g_c$ is canopy conductance (m.s$^{-1}$), $E_c$ is transpiration rate was calculated by $J_S$ and canopy size (L.m$^{-2}$), and all $J_S$ of the four shrubs were standardized as follows:

$$J^*{}_S = \frac{J_S}{LA} \qquad ...(2)$$

Where $J^*_S$ is standardized $J_S$ (L.m$^{-1}$.h$^{-1}$), $J_S$ is sap flow rate (L.h$^{-1}$), *LA* is leaf area of the shrub plant (m$^2$).

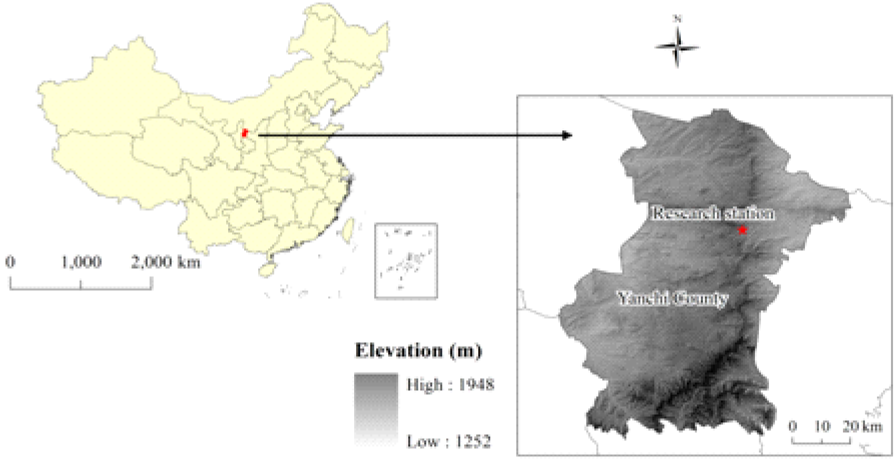

Fig. 1: The experiment site

$$\frac{1}{g_s} = \frac{1}{g_c} - \frac{1}{g_a} \qquad ...(3)$$

Where $g_s$ is canopy stomatal conductance.

$$\frac{1}{g_a} = \frac{\{\ln[(z_h - z_d)/z_0]\}^2}{uk^2} \qquad ...(4)$$

Where $z_h$ is reference height above canopy (m), $z_d$ is shift height (m), $z_d$=0.67 $h_c$, $h_c$ is average height of canopy (m), $z_0$ is roughness (m), $z_0$ = 0.123 $h_c$, $k$ is karman constant number (0.41).

**Statistical analysis:** The data processes and plotting were completed with version 21.0 of the SPSS software (IBM Inc., NC, USA) and OriginPro 9.0 SR2 (OriginLab Inc., Northampton, MA, USA).

## RESULTS AND ANALYSIS

**Environmental variables:** During the study period (day of year, DOY 131-290) in 2011. Precipitation averaged 17.52 mm per event. The $W_S$, $T_a$, VPD, RH, and $R_n$ averaged 2.42 m.s$^{-1}$, 13.95°C, 1.06 kPa, 66.63%, and 81.48 W.m$^{-2}$.day$^{-1}$ respectively. Throughout the study. Compared with the other regions such as Shanxi, Gansu provinces of northwestern China, Yanchi County is characterized by summers with long VPD periods and high amounts of $R_n$, $T_a$, and RH (specific data not shown) (Deng et al. 2015).

**Time lags:** During the transpiration processes, the imbalance between water uptake and loss causes transient changes in internal water deficits (Dzikiti et al. 2007, Deng et al. 2015). This imbalance is known as time lag. Time lag may occur because of a high radial hydraulic resistance between the water storage compartments in the stem and the conducting xylem tissue (Deng et al. 2015, Liu et al. 2010). The time lag should be considered to better understand and build an empirical model of $g_s$ response to environmental factors (Melcher et al. 2012). During this study, all $J_S$ data were standardized. All data were converted to the $J_S$ rate per leaf area. The $J_S$ in the stems of all the shrubs and the two main driving forces ($R_n$ and $W_S$) were selected. Furthermore, three typical months were selected to stand for the early, middle, and late growth stages ("a" stands for May, "b" stands for July, and "c" stands for September). By using Pearson correlation analysis (time range from -180 min to 300 min), the time lag values were determined (Fig. 2). The results revealed that, during the study period, the response of $J_S$ lagged far behind $W_S$ but advanced in $R_n$. The coefficient values of $R_n$ were higher than that of $W_S$, indicating that $J_S$ was affected by $R_n$ more than $W_S$ in the daily range (specific data not shown). However, in this context, the time lag can be neglected because of the short time obtained (<20 min), assuming no capacitance or a high resistance to water.

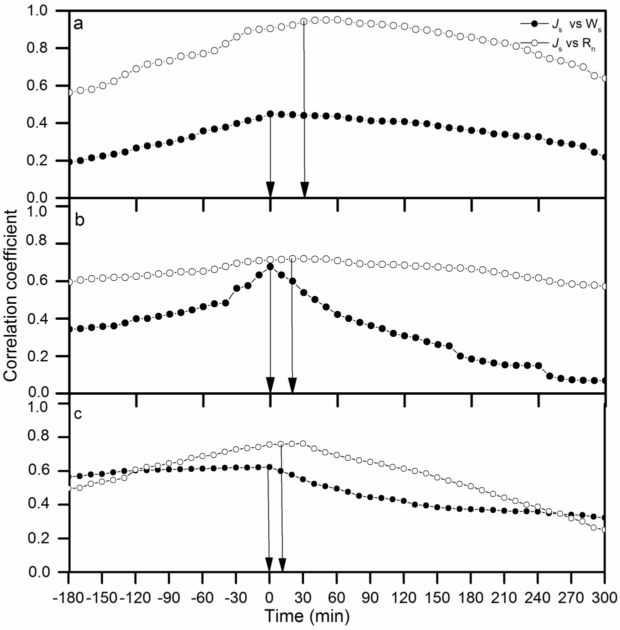

Fig. 2: Correlation analysis between $J_S$, $R_n$, and $W_S$, where "a" stands for May, "b" stands for July, and "c" stands for September.

**Canopy stomatal conductance response to meteorological parameters:** Pearson correlation between $g_s$ and meteorological parameters given in Table 1 reveal that meteorological factors have a significant effect on $g_s$. The order of the meteorological factors is $R_n$ > VPD > $T_a$ > $W_S$ > RH.

$R_n$ can affect $T_a$ directly and RH. VPD is the combination of $T_a$ and RH, which could potentially effect $g_s$. During this study, the $g_s$ response to VPD and $R_n$ can be described as a positive exponential curve, as follows:

| | | |
|---|---|---|
| | $g_s$=0.209e$^{0.309\text{VPD}}$ | ($R^2$=0.513) |
| 0<$R_n$<200W.m$^{-2}$ | $g_s$=0.176e$^{0.372\text{VPD}}$ | ($R^2$=0.262) |
| 200< $R_n$ <400W.m$^{-2}$ | $g_s$=0.556e$^{0.169\text{VPD}}$ | ($R^2$=0.531) |
| 400< $R_n$ <600W.m$^{-2}$ | $g_s$=0.471e$^{0.188\text{VPD}}$ | ($R^2$=0.540) |
| $R_n$ >600W.m$^{-2}$ | $g_s$=0.336e$^{0.237\text{VPD}}$ | ($R^2$=0.587) |

When 0 < $R_n$ < 200 W·m$^{-2}$, the $g_s$ value was nearly dispersed in two axes (data not shown), and $R^2$ was the smallest; thus, $g_s$ within this range was discarded because of its significant variability. When $R_n$ was greater than 200 W.m$^{-2}$, the $g_s$ response to $R_n$ became less sensitive and VPD became the main driving force.

**Model of canopy stomatal conductance and verification:** The phenomenological model described by Jarvis (1976) provides a practical approach for interpreting field measure-

Table 1: Pearson correlation coefficient of meteorological parameters and $g_s$[a].

| Factors/Items | $W_s$ | $T_a$ | VPD | RH | $R_n$ |
|---|---|---|---|---|---|
| $g_s$ | 0.300* | 0.360** | 0.479** | -0.288* | 0.606** |

[a]The values marked * and ** mean they are significant at $p < 0.05$ and $p < 0.01$, respectively.

ments of $g_s$ in relation to environmental variables (Deng et al. 2015, Totzke et al. 2013). The response of $g_s$ to each environmental variable is described by a nonlinear function, and each variable is assumed to act independently, as follows:

$$g_s = g_{s\max} f_1(Q), f_2(T), f_3(D), f_4(q), \ldots \quad ...(5)$$

In this study, we adopted the phenomenological model to construct a $g_s$ model. Considering all the aforementioned factors, the form of the model is expressed as in formulas 6-9:

According to Jarvis's description, $g_s$ is a function of incident $R_n$, VPD, and $T_a$. In this study, we exclude the $W_S$ and RH factors because of the small $R^2$ value and consider $R_n$, VPD, $T_a$, and leaf area index (*LAI*). Thus, the model can be written as follows:

$$g_s = g_{s\text{-}\max} \frac{LAI}{1 + 0.5LAI} f(R_n) f(T_a) f(VPD) \quad ...(6)$$

Where $g_{s\text{-}max}$ is maximum of $g_s$ (mm.s$^{-1}$), $f(R_n)$ can be written as a Michaelis-Menten equation (Deng et al. 2015):

$$f(R_n) = \frac{R_n}{k_r + R_n} \quad ...(7)$$

$f(T)$ can be described by:

$$f(T) = \frac{(T - T_l)(T_h - T)^a}{(k_t - T_l)(T_h - k_t)^a} \quad ...(8)$$

Where $k_r$ and $k_t$ are constants.

$$a = \frac{T_h - k_t}{k_t - T_l} \quad ...(9)$$

Where $T_h$ and $T_l$ are the upper and lower limits of temperature at which $g_s = 0$, and were taken as 30.24 °C and 17.48°C respectively (Dzikiti et al. 2007).

$f$(VPD) takes the form studied above:

$$f(VPD) = k_1 \exp^{(k_2 VPD)} \quad ...(10)$$

We use the nonlinear least squares method to determine the values of $k_r$, $k_t$, $k_1$, and $k_2$ (uncertainties).

Through model verification using the data crossing and comparing methods, we divided the entire measurement time into two periods according to the plant growth rate, namely, Period A ($n$ = 229, DOY 171-232; fast plant growth rate) and Period B ($n$ = 226, DOY 240-304; slow plant growth rate). Models were built to estimate the uncertainty values by using the data of Periods A and B separately. Then, the data of Periods A and B were substituted to obtain a predicted value of $g_s$. Finally, we compared the predicted $g_s$ and the calculated $g_s$ based on $J_S$ to validate the accuracy of the model.

Table 2 shows that the value of $k_t$ was approximately 0 and that the standard deviation of $k_t$ was relatively high. $k_r$ was the highest among all parameters. This result proves that $R_n$ had a significant effect on $g_s$, whereas $T_a$ had only a slight influence on $g_s$. The results are consistent with the Pearson correlation analysis.

Fig. 3 and Fig. 4 show that the predicted data and the calculated data scatter well along the 1:1 line. Furthermore, the residuals scattered evenly along the $x$-axis. The prediction model obtains good results.

## DISCUSSION

$g_s$ determines the transpiration efficiency of forests and is necessary to understand further the underlying mechanism that controls canopy transpiration by considering the coordination of $g_s$ with whole-tree hydraulic conductance. The most feasible approach, which aims to clarify the underlying mechanism, is to integrate the measurements of $J_S$ and the simultaneous records of meteorological factors. In decades of calculating $g_s$, the Jarvis-type model showed that the most significant effect of different physical driving variables, such as $R_n$ and $T_a$, could be distinguished clearly from the effect of leaf water stress (Totzke et al. 2013, Santiago et al. 2013, Ding et al. 2013, Ding et al. 2013). For this reason, we adopted the Jarvis-type model in the present study.

Given the hydraulic properties of a tree, the relationship between measured $J_S$ and actual transpiration is complex. The time lag in $J_S$ is estimated, as many reports state that $J_S$ and meteorological factors are asynchronous. One reason for this phenomenon is the effect of light on the $J_S$ patterns on different sides of the branches of a tree, in which

Table 2: Fitted value of parameters for model of *H. scoparium.*

| Parameter | All data ($n$=455) | Period A ($n$=229) | Period B ($n$=226) |
|---|---|---|---|
| $k_r$ | 71.529 | 42.193 | 65.529 |
| $k_1$ | 0.001 | 0.001 | 0.001 |
| $k_2$ | 2.975 | 2.920 | 3.050 |
| $k_t$ | 0.008 | -0.147 | 0.082 |
| $R^2$ | 65.8 | 68.6 | 63.4 |

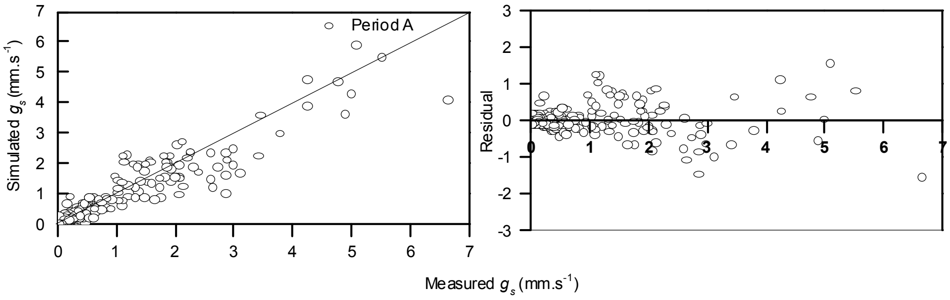

Fig. 3: Relationships between predicted and measured *gs* on Period A (DOY 171-232).

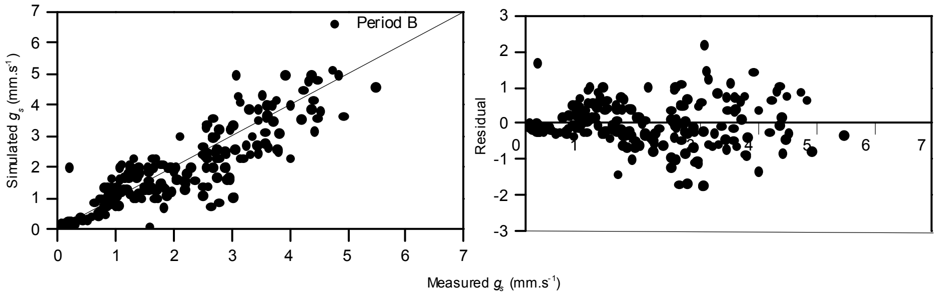

Fig. 4: Relationships between predicted and measured $g_s$ on Period B (DOY 240-304).

the upper, distal, or exposed branches within contiguous forests are illuminated by early morning sun, whereas their counterparts in the canopy remain shaded (Kigalu 2007, Stephen et al. 2008). The other reason is that water flow in the tree encounters different resistances along the conductive pathway. The ongoing transpiration causes a decrease in leaf water potential, which is the driving force for the movement of water through the soil-plant-atmosphere continuum (SPAC system). Together with actual tissue water content, this decrease results in deviations between diurnal courses of $J_S$ and transpiration. Calculating $g_s$ from $J_S$ requires corrections for the lag between water uptake and transpiration (Xia et al. 2008. Yue et al. 2008). Commonly, the lag is estimated from a formal time series analysis of environmental variables and $J_S$. During this research, time lag was less than 20 min, which was considered negligible. We assumed that no time lag occurred in the water transfer from the root to the stem of *H. scoparium*.

Understanding the environmental controls on stomatal conductance has been the central focus of plant interaction with environmental variables for years. In this study, $R_n$, $T_a$, and VPD had the strongest influence on $g_s$ of *H. scoparium*. Many scientists determined that VPD is one of the most important environmental variables that influence stomata (Deng et al. 2015, Kigalu 2007, Yue et al. 2008, Ding et al. 2010, Manzoni et al. 2013, Quentin et al. 2012). Stomata generally close as VPD increases, and the response is often depicted as a nonlinear decline in $g_s$ with the increase in VPD. The magnitude of the reduction or the slope of the stomatal conductance to VPD relationship reflects the response sensitivities. Furthermore, VPD and its interaction with $T_a$ are critical factors that influence stomatal conductance. Plants commonly experience partial or complete stomatal closure during the middle of the day. When $R_n$ is abundant, stomatal closure is mediated by humidity in the atmosphere at the leaf surface. However, the exact mechanisms of these responses are still under debate (Deng et al. 2015, Yue et al. 2008). $g_s$ varied with $R_n$ and $T_a$. Increases in $R_n$ and $T_a$ during the daytime will induce stomatal opening, which can accelerate $J_S$ because of high evaporative demand from the canopy (Yue et al. 2008).

In general, many factors affect $g_s$ simultaneously; thus, a single factor can hardly reflect its relationship. The Jarvis-type model performs well in predicting $g_s$ while considering $R_n$, $T_a$, VPD, and *LAI*. The same method can be applied in modelling the $g_s$ of *Camellia sinensis*, *Caragana korshinskii*, *Caragana microphylla*, *Eucalyptus globulus* and *Betula pendula* (Kigalu 2007, Xia et al. 2008, Yue et al. 2008, Õunapuu et al. 2013).

## CONCLUSION

Our study aimed to set up a Jarvis-type model of canopy stomatal conductance in the *Hedysarum scoparium* shrub and applied the model to predict long-term trend variations. The main findings are listed as follows:

1. The meteorological variables were significantly correlated with canopy stomatal conductance, which increased exponentially with the increase in vapour pressure deficit, with the additional effects from air temperature and solar radiation.
2. The Jarvis model was set up to express the variation observed in canopy stomatal conductance, and the sequence affecting the accuracy of the model was solar radiation > vapour pressure deficit > air temperature.

The main innovation of this study is the analysis of the Jarvis-type model of canopy stomatal conductance in *Hedysarum scoparium* shrub based on sap flow data for the first time. However, its limitation is the lack of consideration for many influencing factors like wind velocity, soil water content, etc. The limitations of this study will be addressed in future studies. Overall, the results of this study can give a better understanding of transpiration by desert plants such as *Hedysarum scoparium* and thus, provide useful information for better afforestation, desertification combating and environmental protection in semiarid region in China.

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