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Seasonal variations and environmental control of water use efficiency in subtropical plantation

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Abstract To understand the seasonal variations of water use efficiency (WUE) of coniferous plantation in the subtropical monsoon area, the experiment was conducted in 2003 and 2004 which presented two distinguished climatic conditions (severe summer drought in 2003 and normal climatic condition in 2004). The water stress influenced WUE greatly, which caused a special seasonal WUE pattern. WUE reached the minimum in summer drought and the maximum in winter, which was contrary to the variation of gross primary production (GPP) and canopy evaporation (Fw). In winter, GPP and Fw increased along with the increasing of air temperature and vapor pressure deficit (VPD), with the similar increasing rate. However, in drought summer, there was an adverse trend among GPP/Fw and air temperature and VPD, and the decreasing rate of GPP was far larger than that of Fw. In summer, the conservation of WUE was changed because of the environmental factors, resulting in the decreasing WUE. The photosynthesis and transpiration of vegetation were mainly controlled by the environmental factors in winter, and the impact of stomatal regulation was relatively weak. In summer, Fw was mainly controlled by the stomatal closure and GPP by both environmental factors and stomatal closure.

Keywords: water use efficiency, gross primary production, canopy evapotranspiration, canopy conductance, eddy covariance.

Water use efficiency (WUE) is an important physiological ecological index to assess the vegetation response to the drought, and it is one of the crucial parameters to evaluate the vegetation productivity and enact water resources policy[1]. Along with global warming, the frequency of drought occurring is increasing[2], even in the place without extreme drought event; the temporal distribution of precipitation could be fluctuated in one year[3]. The climate changing will undoubtedly bring serious impacts on vegetation growth[4,5].

Qianyanzhou Station belongs to Southeast Asia subtropical monsoon area, which is characterized by more precipitation in spring and less in summer and autumn. Consequently, summer drought usually occurs in this area induced by the uneven temporal distribution of precipitation, which is similar to the Mediterranean climate. The vegetation is always suffered from water stressed in this area. Many literatures have reported the impact of Mediterranean drought on vegetation[6−8], but the similar studies were scare in East Asia.

The exchange processes of water and carbon between vegetation and atmosphere are mainly controlled by the environmental and physiological factors. Vapor pressure deficit (VPD) is a main environmental factor for the WUE research[9−11], and stomata were usually considered as an essential physiological factor[12,13]. Photosynthesis is controlled not only by the CO_2 supply process, but also by the CO_2 demand process[14]. However, transpiration was mainly controlled by the stomatal behavior[15]. Therefore when we discussed the controlling mechanism of environmental factors and physiological factors to WUE, two processes should be taken into account: one is how the stomatal behavior affects the diffusion of CO_2 and water vapor; another is how the internal biochemical processes affect photosynthesis[14]. The crop WUE was usually calculated in a special period by crop harvesting; however, there were few studies on WUE using continuous measurements. There were continuous data for almost three years on the carbon, water and heat flux measurement over coniferous plantation in Qianyanzhou Station, which provided plenty of information for analyzing the seasonal characteristics of WUE in different years.

The objectives of this paper are: (1) understanding the seasonal variation of WUE at subtropical coniferous plantation using the eddy covariance measurement; (2) analyzing the impacts of drought on vegetation WUE; (3) discussing the limitation of environmental and physiological factors on WUE to elucidate the determining factor on WUE in Qianyanzhou Station.

1 Site and methods

1.1 Study site

The Qianyanzhou Experimental Station (115°04′13″E, 26°44′48″N) is located at the typical red earth hilly region in the mid-subtropical monsoon landscape zone of South China. According to the statistics of meteorological data from 1985—2002, the mean annual temperature is 17.9℃, annual precipitation 1542.4 mm, annual evaporation 1110.3 mm, mean relative humidity 84%. The coniferous forest was mainly planted after 1985. The forest canopy vegetation is dominated by *Pinus massoniana Lamb*, *Pinus elliottii Engelm*, *Cunninghamia lanceolata Hook*, *Schima crenata Korthals*, *Citrus* L., etc. The evergreen vegetation covers about 76% of the whole canopy.

1.2 Eddy covariance technique

In this research, we applied eddy covariance technique to measuring carbon, water vapor and heat flux. The detailed information about the equipments and principles of eddy covariance technique was described in the literatures of Liu[16], Wen[17] and Song[18].

1.3 Canopy resistance calculations

Penman-Monteith equation was always used to calculate the canopy resistance/conductance,

$$r_{cw}^{c}=\frac{1}{\gamma r_{aw}^{c}}\left(\frac{\Delta R+\rho C_{p}Dr_{a}}{\lambda E_{p}}\Delta\gamma\right), \qquad (1)$$

where r_{cw}^{c} is the canopy resistance for water vapor ($s\cdot mm^{-1}$), r_{cw}^{c} the reverse of g_{cw}^{c}, γ the psychometric constant ($kPa\cdot K^{-1}$), r_{aw}^{c} the aerodynamic resistance ($s\cdot mm^{-1}$), R the net radiation flux at the reference height ($W\cdot m^{-2}$), ρ the air density ($kg\cdot m^{-3}$), C_p the special heat at constant pressure ($kJ\cdot kg^{-1}$), D the vapor pressure deficit at the reference height (kPa), Δ the mean rate of change of saturated vapor pressure with temperature ($kPa\cdot K^{-1}$), and λE_p the water vapor flux measured by eddy covariance technique ($W\cdot m^{-2}$).

r_{aw}^{c} was calculated using Monin-Obukhov similarity theory in neutral conditions,

$$r_{aw}^{c}=\frac{\ln[(z-d)/z_0]\ln[(z-d)/z_{ov}]}{k^2u}, \qquad (2)$$

where z is the reference height of wind speed (m); d the zero plane displacement of forest, which is supposed to be 0.81 time the height of canopy (m); z_0 the roughness length of forest (m), which is supposed to be 0.1 time the height of canopy (m); z_{ov} the water vapor roughness length (m), which is supposed equal to 0.01; k von Karman's constant, 0.4; u the wind speed at reference height.

1.4 Flux data and WUE calculations

The WUE was calculated as the ratio of GPP to ET in this study. The carbon flux measured by eddy covariance technique was net ecosystem carbon exchange (NEE) (negative to net ecosystem productivity, NEP), and GPP was the summation of NEP and ecosystem respiration (Re). For the drought event, we considered the impact of water condition on Re for calculating the Re, and the Q_{10} model could be used to exactly evaluate the Re at this site[19].

The data were dealt as the following processes: (1) Half-hour flux data were rotated with 3D-rotation; (2) the CO_2 and H_2O density fluctuation caused by water and heat were corrected with Webb equation; (3) we eliminated the abnormal data and the data during the period of inadequate turbulence ($u_* < 0.2\ m \cdot s^{-1}$) in the half-hour time series; (4) we filled the carbon and water flux data gap with look-up table method.

In order to reduce the contribution of the evaporation component of ET (ET component from soil surface), the data recorded in the days with precipitation and the day after a rain event were excluded. The daily average was calculated for the periods between 10:00 —16:00.

2 Results and discussion

2.1 Climatic conditions

The study site, Qianyanzhou, is located in the monsoon area, and the precipitation mainly distributes in spring and early summer (Fig. 1). According to the statistics of 18-year (1985—2002) normals in the region, the precipitation mainly concentrated in March, April, May and June, and the highest temperature occurred in July and August. The temporal lag between precipitation and temperature usually resulted in summer drought. Fig. 1 showed that the temperature and precipitation were very close to the average level in 2004, except the less precipitation in October than normal. In 2003, the precipitation was abundant in May, but it was less than the average level of other months, especially in July. Compared with the average level, the summer of the year 2003 was hotter and drier, and the temperature was 3℃ higher than normal, but precipitation, less than 5 mm, was only 23% of the average magnitude in July. Therefore, there exists a severe summer drought in 2003, but it is relatively normal in the same period of 2004.

The seasonal variations of net radiation (R_n), soil moisture content (Sm) and vapor pressure deficit (VPD) were presented in Fig. 2. The largest values of Rn, VPD and the smallest Sm simultaneously occurred in July, 2003. The soil moisture content was relatively low in summer, but high in spring. During the severe drought period in 2003, Sm kept a low level in this station after July, 2003. The smallest Sm appeared in July 2003, July 2004 and October 2004.

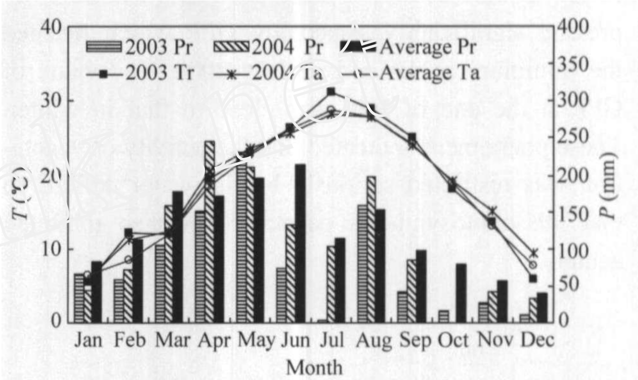

Fig. 1. Comparison of mean monthly temperature and precipitation of 2003, 2004 and previous 18-year normals (1985—2002).

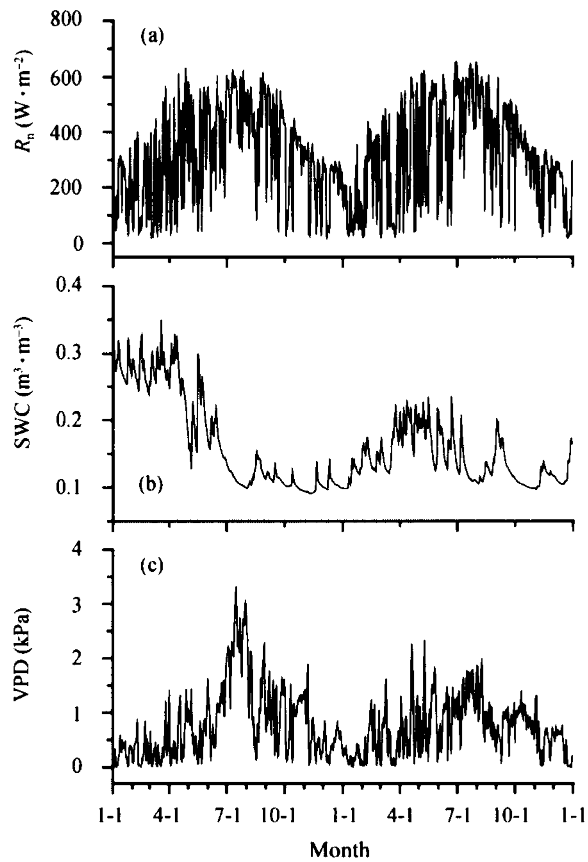

Fig. 2. Meteorological condition in 2003 and 2004. (a) Net radiation; (b) soil moisture content; (c) vapor pressure deficit.

2.2 Seasonal variations of GPP, water vapor flux and WUE

Fig. 3 showed the seasonal variations of GPP, Fw and WUE. The maximum value of Fw appeared in August 2004 and GPP in May 2003. In 2004 the relatively small value of GPP maybe was caused by the severe drought in 2003, and the vegetation growth could not recover in a short time in a normal season. In the drought season of 2003, GPP and Fw were depressed significantly, especially GPP which reached the minimum at the end of July 2003. The value of GPP at the end of July was close to that in winter. These phenomena indicated that the activity of vegetation was restricted seriously by the water deficit, so that the photosynthesis capacity was also inhibited acutely.

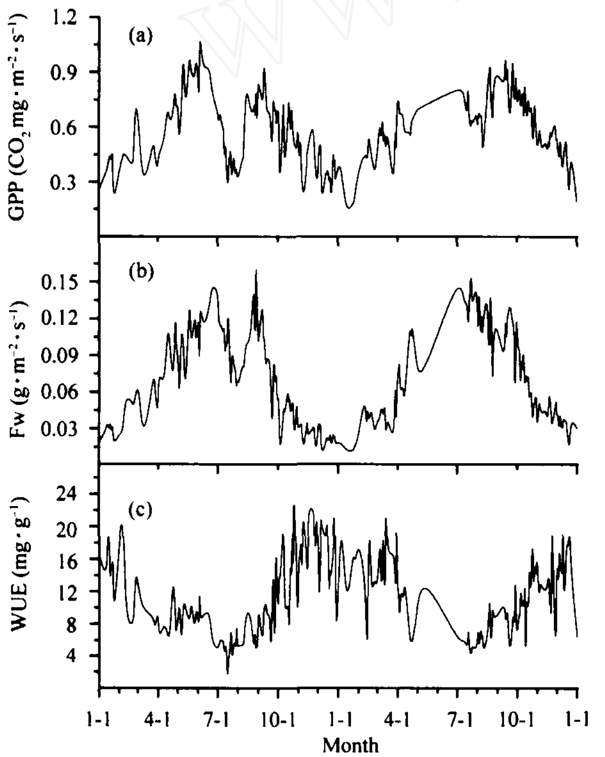

Fig. 3. Seasonal variations of GPP, Fw and WUE in 2003 and 2004. (a) GPP; (b) Fw; (c) WUE.

The seasonal variations of WUE were shown in Fig. 3(c). The value of WUE in summer was lower than that in winter, and it attained the minimum in July 2003, less than 8 mg CO_2/g H_2O, and reached the maximum in December.

In the normal year of 2004, both GPP and Fw attained the maximum in summer and the minimum in winter, GPP decreased in the dry month October, and at the same time Fw was relatively stable. Fig. 3(c) showed that the WUE reached the minimum in dry condition in this station, and this phenomenon was contrary to previous researches[20]. However, the pre-researches focused on the leave level in a short term. Feedback processes can also cause leaf level responses to vary from that observed at the canopy scale[21]. At the ecosystem level, interactions among stomatal conductance, aerodynamic conductance, entrainment of dry air in the planetary boundary layer and changes in leaf temperature can compensate each other so that evapotranspiration is increased despite stomatal closure[22]. Thus canopy or ecosystem WUE should be negatively correlated with variation in the VPD[11], and this relationship was approved in this study (Fig. 4).

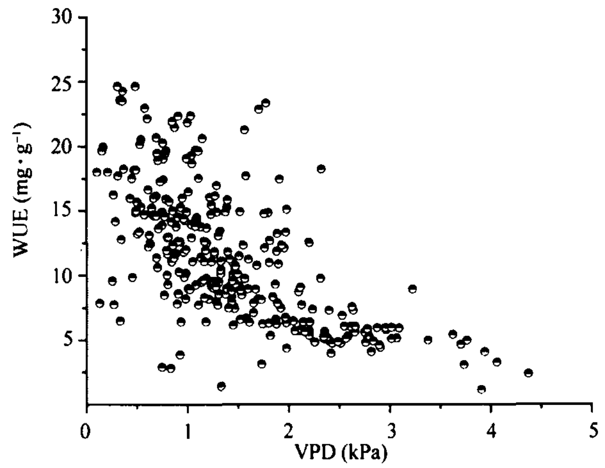

Fig. 4. Response of WUE to VPD.

2.3 Environmental control on WUE

VPD is an important parameter reflecting the air temperature and humidity, and it closely relates to the evaporation from surface (soil and vegetation surface) and transpiration from vegetation, therefore it should be correlated between VPD and WUE. Previous report illuminated a negative correlation between VPD and WUE[11], which was consistent with this research.

WUE gradually decreased from winter to summer in this ecosystem, especially in July and August, WUE reached the minimum; while in December and January, WUE reached the maximum. To analyze the controlling mechanism on WUE, we analyzed the influence of environmental factors on WUE during two contrast periods, summer drought stress and winter droughtfree periods.

To understand the controlling factors on WUE, we analyzed the responses of GPP and Fw to VPD and canopy conductance in winter and summer (Fig. 5), respectively. In winter, GPP and Fw increased significantly along with the VPD ascending (Fig. 5(a)), but showed no obvious relationship to canopy conductance (Fig. 5(b)), which suggests that the photosynthesis and transpiration were controlled mainly by environmental factors, but weakly influenced by stomatal regulation.

In a summer drought period, GPP decreased along with VPD increasing, however, Fw was insensitive to VPD (Fig. 5(c)). Canopy conductance controlled GPP and Fw significantly, and when canopy conductance was less than 8 mm·s^{-1}, GPP and Fw increased along with the augment of canopy conductance (Fig. 5(d)). Fw was mainly controlled by stomatal regulation, and GPP was controlled by stomatal regulation and external environmental factors. When canopy conductance was less than 8 mm·s^{-1}, the responses of photosynthesis and transpiration were similar to stomatal behavior, but different to VPD in a drought condition. The reasons maybe lie in the disorder of physiological and biochemical processes under the condition of high temperature, drought and intensive radiation, and hence the photosynthesis was inhibited. Only considering the limitation of stomatal behavior was incorrect in assessing the inhabitation of photosynthesis. Under the condition of high temperature and drought, the stress from external environmental factors disorganized the internal physiological processes, resulting in more effects on photosynthesis than on transpiration, at last leading to the decreasing of WUE in a drought period.

Because the VPD increased along with the temperature ascending following a certain relationship, water and carbon flux responded to temperature following similar patterns. In this study, the responses of GPP and Fw to air temperature were similar to that to VPD (Fig. 6(a) and (b)). In winter, there were significantly positive relations among air temperature and GPP and Fw with similar slopes. In summer, GPP and Fw decreased along with the increasing of air temperature, and the sensitivity of GPP to air temperature was

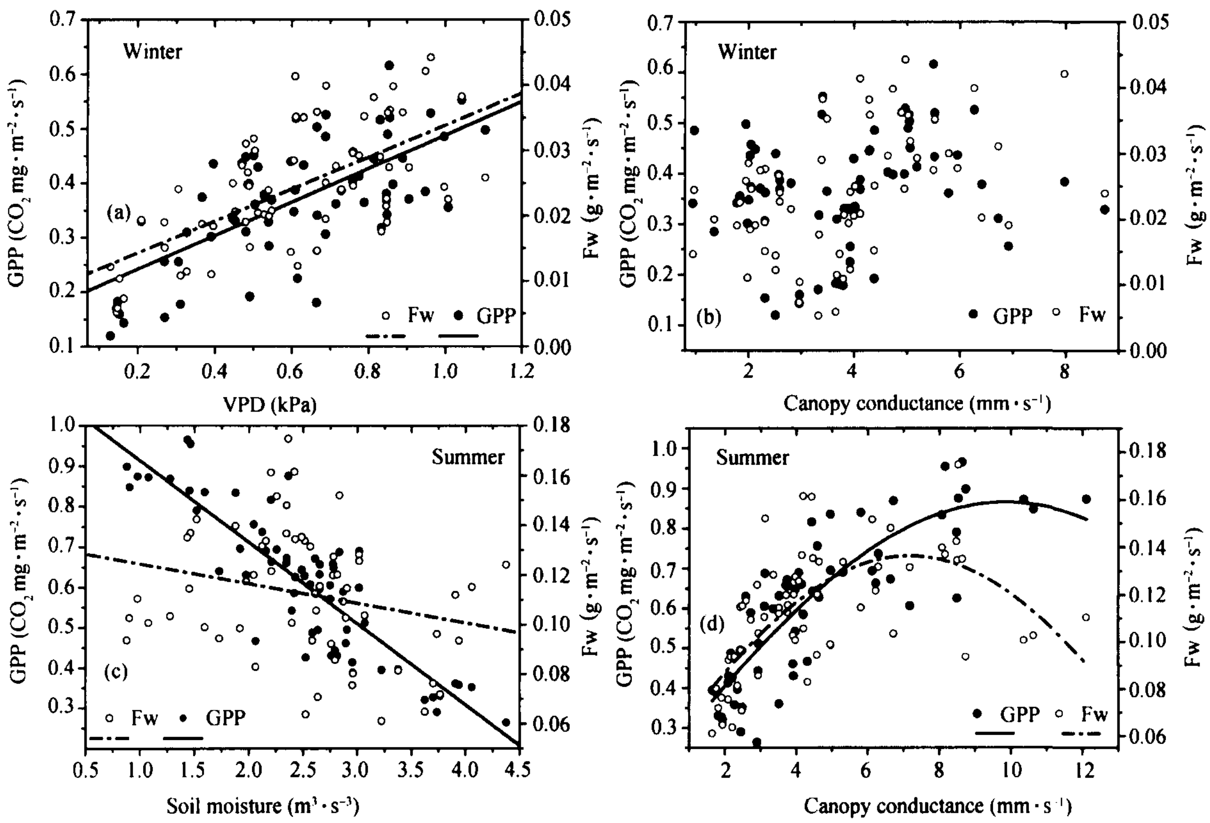

Fig. 5. Responses of GPP and Fw to vapor pressure deficit (VPD) and canopy conductance in summer and winter. (a) GPP and Fw response to VPD in summer; (b) GPP and Fw response to canopy conductance in summer; (c) GPP and Fw response to VPD in winter; (d) GPP and Fw response to canopy conductance in winter.

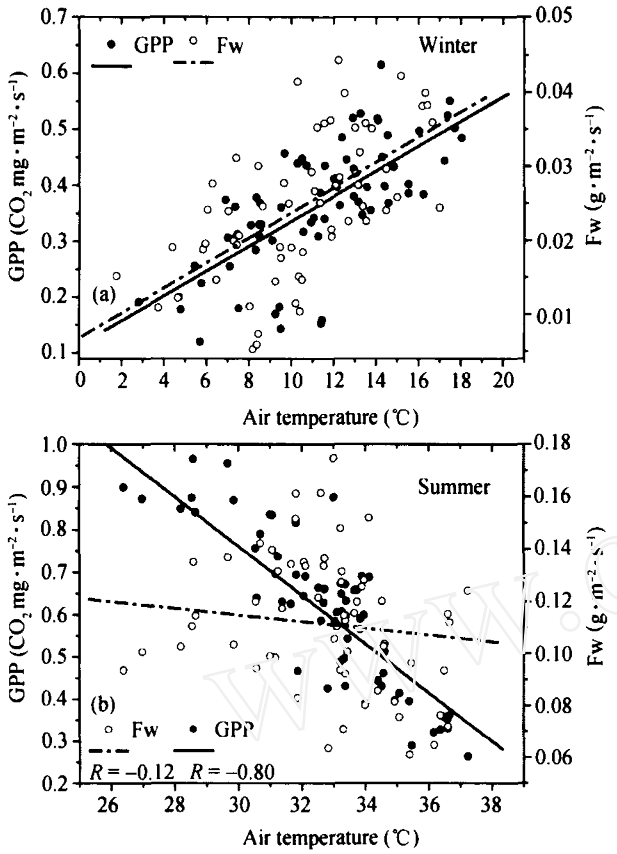

Fig. 6. Responses of GPP and Fw to air temperature in summer and winter. (a) GPP and Fw response to air temperature in winter; (b) GPP and Fw response to air temperature in summer.

higher than that of Fw, which suggests that temperature was the main environmental factor influencing water and carbon flux. So the high temperature inhibited the photosynthesis much greater than transpiration (Fig. 6(b)), leading to the special WUE seasonal variations.

In order to understand the effects of different environmental factors on GPP and Fw, we analyzed the response of GPP and Fw to other environmental factors. In a summer drought period, GPP and Fw were also sensitive to soil moisture, and net radiation in winter.

In a summer drought period, GPP and Fw both increased along with soil moisture ascending (Fig. 7(a)), but the increasing rate of GPP was larger than that of Fw. Consequently, the soil water deficit also limited the capability of photosynthesis and transpiration, and the effect of soil water deficit on photosynthesis was severer than that on Fw. So soil water deficit was one of the reasons which induced the low value of WUE.

In winter, when R_n was less than 300 $W \cdot m^{-2}$, GPP and Fw increased along with the augment of net radia-

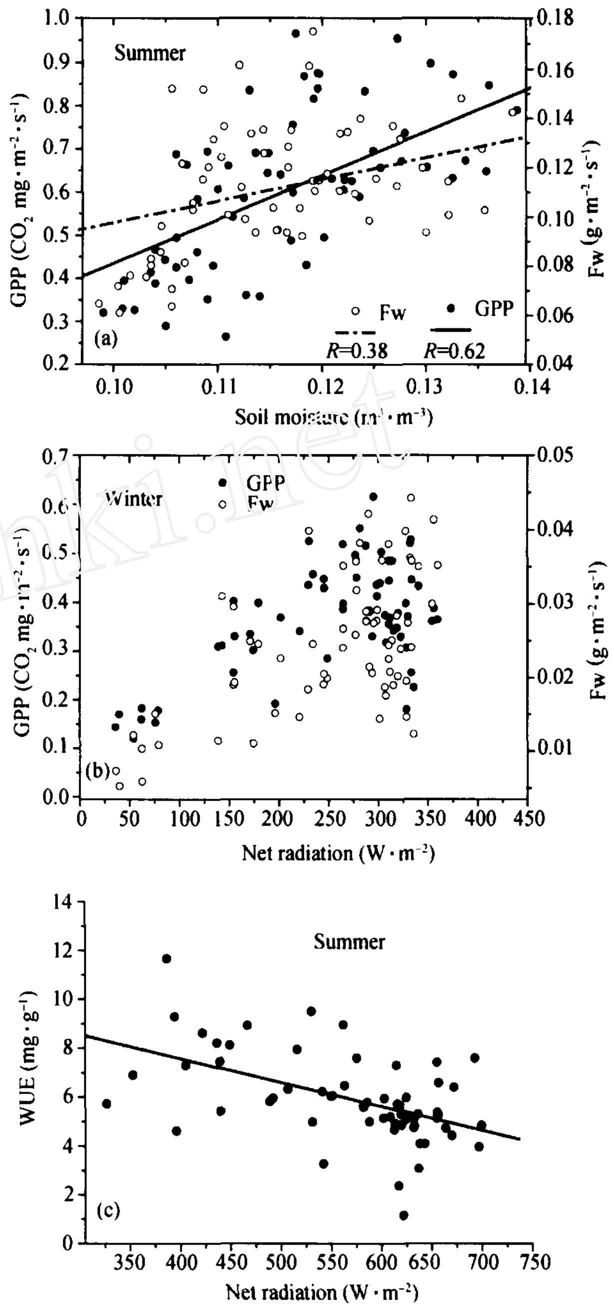

Fig. 7. Responses of GPP and Fw to soil moisture and net radiation and responses of WUE to net radiation in summer and winter. (a) Responses of GPP and Fw to soil moisture in summer; (b) responses of GPP and Fw to net radiation in winter; (c) responses of WUE to net radiation in summer.

tion (Fig. 7(b)), while it was reverse when R_n was larger than 300. Therefore, there should be photo-inhibition in this ecosystem. However, in summer, the net radiation was very strong, so the photo-inhibition may be severer. There were no obvious relationships among GPP/Fw and net radiation, but there was a negative correlation between WUE and net radiation in summer, and therefore the intensive radiation also conduced to the decreasing of WUE.

In summary, there was a similar response mode of GPP/Fw to air temperature and VPD. In winter, GPP/Fw increased along with the increasing of air temperature and vapor pressure deficit (VPD) with similar changing rates. However, in summer drought, there was an adverse trend among GPP/Fw and air temperature and VPD, and the decreasing rate of GPP was far larger than that of Fw. In summer, the conservation of WUE was changed caused by the controlling of environmental factors, resulting in the decreasing WUE.

In addition, the photosynthesis and transpiration of vegetation were mainly controlled by the environmental factors in winter, and the impact of stomatal behavior was relatively weak. In summer, the high temperature and drought stress caused the closure of stomata, and therefore, Fw was mainly regulated by stomatal behavior, and GPP was influenced by both environmental factors and stomatal regulation. Under the condition of high temperature, drought and intensive radiation, GPP was also controlled by environmental factors caused by the disorder of physiological and biochemical processes.

Numerous studies have showed that the pattern of precipitation will change greatly in East Asia along with the global climate changing. On one side, total precipitation will increase[23], meanwhile the summer drought will become severer caused by the temporal fluctuation of precipitation in a year[24]. Therefore, the limitation of severe drought on GPP and Fw will be severer in the future scenario, and the WUE will be a focus in the near future.

3 Conclusions

In this paper, by analyzing the seasonal variations of GPP, Fw and WUE over plantation in Qianyanzhou Station, we discussed the influence of environmental factors on GPP, Fw and WUE in summer and winter, and drew several conclusions as follows:

For the uneven temporal distribution of precipitation, there was usually an obvious seasonal drought in Qianyanzhou Station. This seasonal drought will affect carbon and water budget seriously.

The seasonal variation pattern of WUE was reverse to those of GPP and Fw. WUE reached the minimum in a summer drought period and the maximum in winter.

The response mode of GPP to air temperature and VPD was similar to that of Fw. In winter, GPP and Fw increased along with the increasing of air temperature and vapor pressure deficit (VPD) with similar changing rates; while in summer drought, there was an adverse trend. In summer, the conservation of WUE was changed under the influence of severe environmental factors, resulting in the decreasing WUE.

In addition, the photosynthesis and transpiration of vegetation were mainly controlled by the environmental factors in winter. In summer, Fw was mainly regulated by stomatal behavior, and GPP was influenced by both environmental factors and stomatal regulation.

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