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RESEARCH ARTICLE

Drought resistance of four grasses using pressure-volume curve

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Abstract Pressure-volume curve (PV curve) technique is a major method for studying critical plant water potential and critical tissue water content when plasmolysis takes place. In the present study, a mathematical solution method is put forward to obtain parameters based on the PV curve. The calculated results for the parameters of *Lolium perenne, Festuca arundinacea, Leymus chinensis* and *Stipa krylovii* indicated that the mathematical solution method is convenient for actual research compared with the graphical method. Further analysis of the calculations suggested that drought resistance decreased in the following order: *S. krylovii* > *F. arundinacea* and *L. chinensis* > *L. perenne*.

Keywords pressure-volume curve, water potential of plant, plasmolysis, index of drought resistance

1 Introduction

When saturated leaves are placed in a Scholander pressure chamber (Scholander et al., 1964), the continuous pressure received changes the osmotic water quantum, and under these conditions, the relationship between the osmotic water quantum and the reciprocal of the corresponding equilibrium pressure is described as the pressure-volume curve (PV curve). The PV curve technique was first reported by Scholander (Scholander et al., 1965), then improved on and supplemented by Tyree et al. (1972; 1973; 1976; 1981; 1982), Cheung et al. (1975; 1976), Richter et al. (1973; 1978; 1990) and Schulte and Hinckley (1985). This technique is frequently used to study water relations of plants (Roberts and Knoerr, 1977; Wenkert et al., 1978; Rygol and Luttge, 1983; Sinclair and Venables, 1983; Li, 1989; Feng, 1995; Beckett, 1997; Dong et al., 1999; Tomos and Leigh, 1999; Wang et al., 1999; Willigen et al., 2001) and cell wall elasticity (Stadelmann, 1984; Steudle et al., 1983; Wu et al., 1985; 1988; Shen and Li, 1994; Spence and Wu, 1995). Currently, the PV curve technique is still a major method for studying plant water relationships since there is no proper theoretical method to calculate for the critical plant water potential and critical tissue water content during plasmolysis (Wang, 1984).

In previous studies, the parameters of the PV curve were based on graphic analysis (Wang, 1984), hereafter mentioned as the graphical method. One of the most important problems of the graphical method, however, is that it is difficult to precisely determine the critical values of the osmotic potential and the relative water deficit when pressure potential is reduced to zero, i.e. to accurately ascertain the critical point when plasmolysis takes place. Some errors due to the subjective judgment of the point restricts its proper use (Tyree and Hammel, 1972; Cheung et al., 1975; Richter, 1978; Wang, 1984). Such potential problems associated with the graphical method necessitate actual research to improve this method. In the present study, we put forward a mathematical solution method for the PV curve, by studying drought resistance of four species of grass, *Lolium perenne, Festuca arundinacea, Leymus chinensis* and *Stipa krylovii* based on PV curves.

2 Materials and methods

2.1 PV curve and improvement of current methods

There have been many reports on the mathematical theory of the graphical method of the PV curve (Scholander et al., 1965; Tyree and Hammel, 1972; Richter, 1978; Wang, 1984). According to such reports, the graphical method involves two ways of making graphs: (1) a graph on the interrelation between the reciprocal of plant water potential and the

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relative water content, and (2) a graph on the interrelation between the reciprocal of plant water potential and the infiltration water quantum (Richter, 1978; Wang, 1984). In the present study, the latter method was used (Fig. 1). In Fig. 1, all the observed data points are connected to form a curve; when turgor is lost, the corresponding observed data points form a straight-line regression. The graphical method (Wang, 1984; Li, 1989; Feng, 1995) extends from both ends of the regression line. Its intersection with the x-axis shows a dividing point between symplast water (free water, V_f) and apoplast water (bound water, V_b) in tissue, and its intersection with the y-axis is the reciprocal of the osmotic potential at full turgor ($\Psi\pi^{100}$). The intersection of the beeline and the curve shows the critical water status when turgor is completely lost. At this point, the values of the x-axis and the y-axis show the reciprocal of the critical osmotic water quantum (V') and the critical water potential (Ψ'), respectively. The percentage of the critical osmotic water quantum in the total tissue water content is defined as the critical relative water deficit (RWD_0). From these, other parameters can also be calculated.

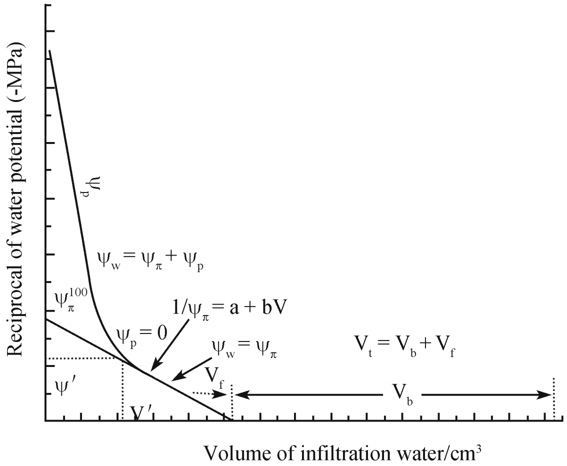

Fig. 1 Graphical method of pressure-volume curve

In a previous study (He et al., 2001), the PV curves of 16 plant species were fitted as the power functions, and showed significant regression correlations. In this experiment, the same was seen for the four grasses (Table 1). Thus, the PV curve can be expressed as a power function curve. Below their intersection, the PV curve and the beeline generally overlap each other so that plant water potentials equal the osmotic potentials at this point. We can thus obtain the critical value of the relative water deficit (V', the intersection value on the x-axis) by solving for the intersection value of the power function ($1/\Psi_\omega = aV_1{}^b$) and the regression line ($1/\Psi_\pi = c + dV_2$).

As a result, the PV curve can be expressed as the equation $1/\Psi_\omega = aV_1{}^b$, and the beeline can be expressed as the equation $1/\Psi_\pi = c + dV_2$. In order to solve for the intersection value of the two functions, we must satisfy the following mathematical conditions:

$$\begin{cases} aV^b = c + dV & (1) \\ (aV^b)' = (c + dV)' & (2) \end{cases}$$

where equation (2) has a unique solution:

$$V = \sqrt[b-1]{\frac{d}{ab}} \tag{3}$$

Considering mathematical strictness, by substituting equation (3) into equation (1), we can get the following

$$\left(\frac{1}{b} - 1\right)\left(\frac{d}{ab}\right)^{\frac{1}{b-1}} = \frac{c}{d} \tag{4}$$

If parameters a, b, c, and d can satisfy equation (4), then equations (1) and (2) can be solved.

In this instance, critical osmotic water quantum is solved as follows:

$$V' = \sqrt[b-1]{\frac{d}{ab}} \tag{5}$$

where V' is the critical infiltration water, g.

After solving for the parameters of the four grasses in Table 1, we found that they all easily satisfied equation (4) (the error is smaller than 10^{-4}).

Now, substituting the V' obtained from equation (5) into the equation $1/\Psi_\omega = aV_1{}^b$, we get the critical osmotic water potential Ψ' (MPa)

$$1/\Psi' = aV'^b \tag{6}$$

In all the above equations, a, b, c, and d denote the parameters in the power function and the beeline function.

Table 1 Regression relationships of pressure-volume curves for four grasses

Species	PV curves		Regression straight lines	
	Equation	R^2	Equation	R^2
Lolium perenne	$1/\Psi_\omega = 0.069V_1^{-0.491}$	0.972**	$1/\Psi_\pi = -10.120V_2 + 0.669$	0.829**
Festuca arundinacea	$1/\Psi_\omega = 0.0439V_1^{-0.659}$	0.981**	$1/\Psi_\pi = -17.640V_2 + 0.939$	0.743*
Leymus chinensis	$1/\Psi_\omega = 0.0065V_1^{-1.151}$	0.953**	$1/\Psi_\pi = -21.750\ V_2 + 0.992$	0.802**
Stipa krylovii	$1/\Psi_\omega = 0.1006V_1^{-0.223}$	0.970**	$1/\Psi_\pi = -5.179V_2 + 0.331$	0.796*

Note: where Ψ_ω is plant water potential (MPa); V_1 is volume of infiltration water corresponding Ψ_ω (cm^3);
Ψ_π is osmotic potential (MPa); V_2 is volume of infiltration water corresponding Ψ_π (cm^3);
**Stands for significance at 0.01 level; *at 0.05 level.

Based on the PV curve principle and from the linear regression equation $1/\Psi_\pi = c + dV_2$, when $V_2 = 0$ (the point where the line intersects the y-axis), we can calculate for the reciprocal of the osmotic potential Ψ_π^{100} (MPa) when the plant tissue has the largest turgor pressure, thus:

$$1/\Psi_\pi^{100} = c \tag{7}$$

Meanwhile, results from our experiment showed that when the equilibrium pressures were constant, the measured osmotic water quantum varied; when the equilibrium pressures were kept stable and the weights of the plant tissues were also unaltered, the infiltrated water volume was 0.18 times higher than the accumulated osmotic water quantum during the period from the first to the last equilibrium pressure. We may also presume that the symplast water content (free water) should equal the sum of all infiltrated water quanta, and can be expressed as follows

$$V_f = 1.18V_e \tag{8}$$

where V_f is the symplast water, g; and, V_e is the total infiltration water quantum, g.

We can then calculate the other parameters

$$V_t = W_s - W_d$$

where V_t is the water content in tissue at saturation level, g; W_s is weight of the tissue after saturation, g; and, W_d is the dry weight of the tissue, g.

Bound water content (V_b, g) can then be described as

$$V_b = V_t - V_f \tag{9}$$

Thus, the critical relative water deficit (RWD_0, %) can be calculated as

$$V_f(\%) = (V_f/V_t) \times 100\% \tag{10}$$

$$V_b(\%) = (V_b/V_t) \times 100\% \tag{11}$$

$$RWD_0 = (V'/V_t) \times 100\% \tag{12}$$

As for the infiltration water quantum at the first equilibrium pressure,

$$V_x = W_s - W_{f1}$$

where V_x is infiltration water quantum at the first equilibrium pressure when the tissue is saturated, g; W_{f1} is the corresponding fresh weight of the tissue at the first equilibrium pressure, g.

As for the osmotic potential at the first equilibrium pressure,

$$1/\Psi_{\pi 1} = c + dV_x$$

In this equation, $\Psi_{\pi 1}$ indicates the osmotic potential at the first equilibrium pressure, MPa; with c and d as earlier described.

As to the pressure potential at full turgor in tissue,

$$\Psi_p^{100} = P_1 - 1/\Psi_{\pi 1} \tag{13}$$

where Ψ_p^{100} is the pressure potential at full turgor in tissue, MPa; P_1 is the first balance pressure, MPa.

Finally, the elastic modulus can be computed as:

$$\varepsilon_{max} = V_f(\Psi_p^{100}/V_x) \tag{14}$$

where ε_{max} is the elastic modulus, MPa.

It should be pointed out that there are many formulae to calculate the elastic modulus (Steudle et al., 1983; Stadelmann, 1984; Wu et al., 1985; 1988; Spence and Wu, 1995; Shen and Li, 1994). At present, there does not exist a formula which is well recognized and accepted by most scholars, thus, in this paper, the original definition (Li, 1989) was adopted.

After entering all the equations into a software program, we only needed to input nine kinds of data: a, b, c, d, W_s, W_d, W_{f1}, V_e and P_1, and the computer calculated the results.

2.2 Data collection

We selected *S. krylovii*, *F. arundinacea*, *L. chinensis* and *L. perenne* as experimental species, which were planted in the experimental field of the ecological laboratory of Nankai University. Among them, *S. krylovii* was introduced from the Ortindag Sandy Land of Inner Mongolia, *L. chinensis* was introduced from the Chi-feng district of Inner Mongolia, *F. arundinacea* (SR4000) was introduced from Australia, and *L. perenne* was introduced from Montana (USA).

The top middle leaves of the four grasses were cut and soaked in water for 24 hours until they were saturated with water. The leaf water potentials were determined by using a ZLZ-5 Pressure Chamber (made in Lanzhou University). The procedures in detail are as follows.

First, after preparation of the saturated tissue samples, their weights were measured using an electron balance for 0.001 precision, and they were placed in the chamber. Pressure was then increased at the speed of 0.3 MPa/min until many bubbles were seen emitting from the cut portions. This indicated that the needed equilibrium pressure was reached. The measured samples were then taken out and weighed one by one. The values were recorded and the samples were placed in the chamber once again. The above procedures were then repeated until a new equilibrium pressure was realized. The equilibrium pressure was increased gradually for 11 or 12 times and the equilibrium pressure and the fresh weight of the samples under different pressures were recorded respectively. Finally, the samples were taken out, their weights were recorded, and then they were dried at 110°C for 6 hours to get the dry weight.

2.3 Data analysis

Using Microsoft Excel 2000, the reciprocals of the equilibrium pressure acted as the dependent variables and the infiltration water quantum under different equilibrium pressures were the independent variables. The infiltration water quantum were input into the first column (as the *x*-value), the reciprocals of all equilibrium pressures were placed in the second column (as the y1-value), and the reciprocals of the equilibrium pressure used for the straight line equation were input into the third column (as the y2-value) where data must correspond with their equilibrium pressure. The equilibrium pressures used to fit into the straight line equation were the last of several data whose varying amplitudes were contiguous and obviously disparate. In this way, we were able to fit the power function and the linear function together, and obtain the regression equations and their coefficients of decision (Table 1).

Following these, nine kinds of data for a, b, c, d, W_s, W_d, W_{f1}, V_e and P_1 were input. In running the program, we were able to get all the parameters of the PV curve and the derivative indices.

2.4 Calculation of the drought resistance indices

The parameters obtained from the PV curve can be used in the analysis of drought resistance (Wang et al., 2000). The formula is listed as follows.

$$DI = \sqrt{\sum_{1}^{n} \left(\frac{p}{p_{\max}} \right)^2}$$

where DI is a dimensionless index of drought resistance; p is the value obtained from calculation of the parameters Ψ_p^{100}, Ψ', Ψ_π^{100}, RWD_0, V_b/V_f, and ε_{max}; p_{max} is the greatest value among them.

Here, the average value of $\bar{p}$ was used to substitute for the largest value p_{max} in the original formula:

$$DI' = \sqrt{\sum_{1}^{n} \left(\frac{p}{\bar{p}} \right)^2} \tag{15}$$

where $\bar{p}$ indicates the average value of the same index for the different plants.

As a result, the improved DI' equation better reflected the actual situation because the new equation considered the inline relationship among the plants being compared.

3 Results and analysis

3.1 Ψ_p^{100}

A larger turgor pressure benefits cell elongation, plant growth, and other physiological and physiochemical process. When plant water potential is reduced, the main mechanism to resist drought is to keep the turgor pressure constant (Wang, 1984). The results of our calculations indicated that *L. chinensis* and *F. arundinacea* had larger turgor pressures (Table 2), and this characteristic enabled them to use their osmotic adjustment capability sufficiently to resist water stress.

Table 2 The parameters based on the PV curves of four grasses

Parameter	*L. perenne*	*F. arundinacea*	*L. chinensis*	*S. krylovii*
Ψ_p^{100}/MPa	0.317	0.627	0.730	0.338
Ψ'/MPa	2.025	1.783	2.156	3.690
Ψ_π^{100}/MPa	1.355	1.066	1.008	3.018
RWD_0/%	28.122	33.886	31.405	39.494
V_f/%	52.590	54.420	43.460	58.800
V_b/%	47.410	45.580	56.540	41.200
V_b/V_f	0.900	0.840	1.300	0.700
ε_{max}/MPa	1.438	5.995	5.061	1.958
DI	1.318	1.802	1.949	1.900
DI'	1.901	2.671	2.844	2.926

3.2 Ψ_π^{100}

The lower the value is, the stronger the ability to forbear dehydration. It shows that the plant will have a denser cell sap at this time, and as a result, leaf growth and physiological activities can progress even with low water potential. Under dry conditions, to keep the turgor constant, a plant has to reduce its osmotic potential in order to absorb enough water from the soil. Obviously, *S. krylovii* possessed dominance in this aspect.

3.3 Ψ'

When plasmolysis takes place, the lower the osmotic potential is, the stronger the ability of the plant to tolerate water stress. Tyree and Hammel (1972) suggested that the drought resistance characteristic of a plant finds expression in the tissue cell which lives in a low osmotic potential, and only in this circumstance would plasmolysis take place. When plasmolysis takes place, the osmotic potential indicates the ability of the tissue cell to resist the lowest possible value. For this character, *S. krylovii* was greater than the three others.

3.4 RWD_0

The greater the critical relative water deficit is, the stronger the response to drought resistance is. From this we found that the response of *S. krylovii* to drought stress was stronger than that of *L. chinensis* and *F. arundinacea*.

3.5 V_b/V_f

In general, plants possess a greater ratio of V_b/V_f under unfavorable environmental conditions. The highest daily and yearly values of this index appear at noon and in summer, respectively (Huang, 1991). Thus, this value is thought to be an important factor in plant drought resistance. For this index, the value from *L. chinensis* was greatest, followed by *F. arundinacea* and *L. perenne*, and *S. krylovii* had the lowest.

3.6 ε_{max}

Roberts et al. (1981) suggested that, the leaf bulk elastic modulus reflects the relationship between the tissue water content and the turgor. Our research further provided evidence that these four grasses had the same changes in trend of the elastic modulus as well as in the turgor (Table 2). In general, the greater the elastic modulus is, the thicker the cell wall is, and the less elastic the cell is; and vice versa. Plants under dry stress have smaller cells and thicker walls, thus they can keep high turgor pressures (Li, 1989). The ε_{max} values of *F. arundinacea* and *L. chinensis* were relatively greater than the others.

3.7 *DI*

In the process of the long period of natural evolution, different plants develop different physiologic and ecologic properties in order to adapt to the environment. From the analysis above, we can say that the four grasses each have their respective advantages in terms of the different indices. Therefore, it is essential to uncover plant drought resistance by comprehensively analyzing these indices from the PV curve. The calculation of DI by using the improved equation (15) indicates that the response of the four grasses to drought stress was in the order: *S. krylovii* > *Leymus chinensis* and *Festuca arundinacea* > *L. perenne*. However, using the original equation, the results are as follows: *Leymus chinensis* and *F. arundinacea* > *S. krylovii* > *L. perenne* (Table2). Obviously, the results calculated by using equation (15) better reflect reality.

4 Discussion

The key problems in using the PV curve technique lie in accurately ascertaining the critical point when plasmolysis takes place and to determine the points where the straight line regression intersects with the ordinate and the abscissa. Sequentially, we can derive the other parameters such as Ψ', V', V_f, Ψ_π^{100}. In this paper, by using the mathematic method, we were able to obtain all the parameters of the PV curve, and the results from using this method are relatively satisfactory. In equation (8), 0.18 is the experience coefficient, but in this study, this equation was replaced by summing up the following values: accumulated osmotic water quantum before the equilibrium pressures are constant and the osmotic water quantum within the period when the equilibrium pressures are constant.

Calculation of the *DI* by using the improved equation (15) showed that the order of drought resistance for the four grasses is: *S. krylovii* > *F. arundinacea and L. chinensis* > *L. perenne.* The results are an objective reflection of the actual situation. For example, the distribution regions of *S. krylovii* are located to the west of those of *L. chinensis* in China. As two important constructive species groups, *S. krylovii* and *F. arundinacea* are influenced by the East Asia monsoon. The farther west the distribution location for constructive species is, the stronger the response to drought resistance by the plant. Thus, the response to drought resistance of *S. krylovii* should be stronger than that of *L. chinensis*. Furthermore, the plant water potential is an index for weighing water status in the plant body, and also serves as an index for weighing the plant's ability to resist drought stress. Our observations showed that the monthly average leaf water potentials of *S. krylovii* and *L. chinensis* were $-(2.59 \pm 0.07)$ MPa and $-(1.94 \pm 0.12)$ MPa, respectively. Because obviously, the plant water potential of *S. krylovii* was lower than that of *L. chinensis*, the response of *S. krylovii* to drought resistance was stronger than that of *L. chinensis*. Finally, the ability for drought resistance of a plant in anaphase is stronger than that of a plant in prophase. Field investigations showed that *L. chinensis* was replaced by *S. krylovii* in the field community, suggesting that the response of *S. krylovii* to drought resistance was stronger than that of *L. chinensis*. Therefore, by using the PV curve technique, we can study the property of plant drought resistance effectively.

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