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Original article

Effects of soil moisture on plant growth and ginsenoside production of *Panax ginseng* C. A. Meyer

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Summary

Ginseng is a perennial plant cultivated as a traditional medicine formulation for human health. Its growth and quality are influenced by environmental factors such as soil moisture, which affects plant morphogenesis and metabolism. Thus, this study identified the effects of soil water on ginseng growth and ginsenoside production by regulating soil moisture conditions. The results showed that the agronomic traits of shoots, roots, fruits, seeds, and ginseng seedlings' survival rates under 0.8 field capacity (FC) were significantly higher than those under 0.4 and 0.6 FC. Severe drought (0.4 FC) was beneficial to accumulating ginsenosides and total ginsenosides. The production of ginsenosides decreased due to the decrease in dry root weight. Excessive water (1.0 FC) was advantageous to the ginseng growth, but made the roots short and thick, and red skin disease infected the roots. Adequate water supply (0.8 FC) produced higher 11 ginsenosides and total ginsenoside than other treatments. 0.8 FC was the most suitable soil moisture condition for ginseng growth. It delayed ginseng wilt, gave the best agronomic traits, and the most ginsenoside production.

Keywords
agronomic trait, ginseng, ginsenoside, plant growth, soil moisture, survival rate

Significance of this study

What is already known on this subject?

- Appropriate water supply represents a critical aspect of plant growth, because water content has effects on plant morphogenesis and metabolism. *Panax ginseng* C. A. Meyer is a perennial herb whose roots have been widely used as a traditional medicine formulation for human health for thousands of years. Systematic studies on the effects of soil moisture on the growth and quality of ginseng have not been reported.

What are the new findings?

- 0.8 FC was the most suitable soil moisture condition for ginseng growth. It delayed ginseng wilt, gave the best agronomic traits, and the most ginsenoside production.

What is the expected impact on horticulture?

- Appropriate soil moisture (0.8 FC) could improve the yield and quality of ginseng, and this result provided vital information that can be used as a guide for a suitable irrigation management program.

Introduction

Panax ginseng C. A. Meyer is a perennial herb belonging to the Araliaceae family, commonly known as Asian ginseng (Chinese Academy of Science, 1978). Its roots have been widely used for thousands of years as traditional medicine such as antioxidative, anticarcinogenic, and antidiabetic effects (Attele et al., 1999; Jung et al., 2020). The primary bioactive ingredients of ginseng are a group of triterpene saponins. It has approximately 30 unique saponins, commonly known as ginsenosides (Chuang and Sheu, 1994). The content of ginsenoside is the most important factor affecting the ginseng medicinal value (Yu et al., 2019), which is influenced by abiotic stresses, including nutrient content (Lee and Mudge, 2013a), light (Fournier et al., 2003), temperature (Hwang et al., 2014; Yu et al., 2005), and soil moisture (Lee and Mudge, 2013b; Lim et al., 2006). Water stress could increase the contents of specific individual and total ginsenosides of American ginseng (Lee and Mudge, 2013b; Lim et al., 2006).

Ginseng is a perennial shade plant, and the phenological period of ginseng growth and development can be divided into seven stages: seedling stage (early May), leaf developing stage (early May to mid-May), flowering stage (early to late June), green fruiting stage (early June to late July), red fruiting stage (early August), post-fruit root growing stage (early August to late September) and wilting stage (mid to late September) (Yang, 2017). According to habitat observations, ginseng plants love water but hate wet and thus grow well in drained places with high soil moisture but are not found in dry or damp areas (Park, 1980). Some studies found that soil moisture showed a significant positive correlation with root yield, stem diameter, and chlorophyll content but a significant negative correlation with the relative missing plant rate (Lee et al., 2007; Park et al., 1982). In addition, American ginseng root diameter and fresh weight decreased with progressive water deficit, while total root length increased with increasing water deficit (Lee and Mudge, 2013b; Li and Berard, 1998). Some ginseng diseases, such as red skin disease, are caused by excessive soil moisture, which may result in poor soil permeability and ventilation, lead to root hypoxia and reductions in metabolism and increase the incidence of root red skin disease (Liu et al., 2014; Park, 1982a; Ricoult et al., 2006).

So adequate soil moisture is considered one of the most critical factors in growing high yields of good-quality ginseng. A long-term systematic water regulation was used to study the effects of soil moisture on the growth and quality of three-year-old ginseng. The observed agronomic traits were shoots, roots, fruits, seeds, the survival rate of ginseng seedlings and the content and production of twelve ginsenosides and total ginsenosides. This study aimed to improve yield and accurately regulate ginsenoside synthesis and accumulation through water regulation and provide a theoretical basis for establishing irrigation rules for standard ginseng cultivation.

Materials and methods

Plant and experimental site

Three-year-old Asian ginseng seedlings with uniform size and no disease were used in this study. The experiment was conducted in the Medical Plant Cultivation Base in Zuojia Town, Institute of Special Animal and Plant Science, Chinese Academy of Agricultural Sciences (44°03'08.0"N, 126°05'24.9"E, altitude 230 m).

Experiment treatment

Plastic frames (6 m length, 1 m width, 30 cm height) were used as experimental units. Each frame was placed in a plastic sheet around and at the bottom and then filled with disinfected soil, which was taken from the idle field.

On May 3, 2020, three-year-old ginseng seedlings were planted in the frames. The plant spacing was 12.5 cm, with eight plants per row, and the row spacing was 20 cm, with a total of 30 rows per treatment. Then, blue plastic sheets and shade nets were used for rain shelter and shade (light transmittance 30%).

Four water moisture gradient treatments were set in this study, namely, 0.4 FC (severe drought) treatment, 0.6 FC (mild drought) treatment, 0.8 FC (adequate water supply) treatment, and 1.0 FC (excessive water) treatment. The soil moisture of 0.4 FC, 0.6 FC, 0.8 FC and 1.0 FC treatments were kept at 40 ± 5%, 60 ± 5%, 80 ± 5% and 100 ± 5% field capacity, respectively. The field capacity was 29.38%, and the initial soil water content was 22.71%, and the initial soil bulk density was 95.5 g cm^{-3}. From May 3, the soil water content of 4 treatments were measured and supplemented by watering every 7 days, while watering was started until the soil moisture of 0.4 FC and 0.6 FC treatments reached the set value. Water supply volume was calculated from measured soil water content, the set soil moisture, the volume of each frame and soil bulk density, and water was supplemented by artificial watering. By June 15, the soil moisture in all treatments reached the set gradient. After that, soil moisture was regulated by regular measurement of soil water content and artificial watering to ensure that soil moisture in different treatment was maintained at the set gradient until September 28. Gravimetric methods confirmed soil water content, soil field water capacity, and soil bulk density were measured by the ring sampler test (Klute, 1986; Liao et al., 2017).

Determination of agronomic traits of ginseng root and aboveground organ

The agronomic traits determined in the present study were as follows: fresh root weight, root dry weight, root length, fibrous root length, root diameter, bud length, bud width, aboveground dry weight (not including flowers or fruit), stem height, stem diameter, petiole length, and leaf area. The area of the largest leaflet in each plant was measured by an YMJ-D leaf area measurement instrument (Zhejiang Top Cloud-Agri Technology Co., Ltd., China); thirty leaves were detected in each treatment. Twenty leaves were randomly selected from each treatment, and the chlorophyll content (SPDA value) was measured by a chlorophyll meter TYS-A (Zhejiang Top Cloud-Agri Technology Co., Ltd.). For dry matter analysis, roots, leaves, and stems of ginseng were dried at 45°C until thoroughly dry.

Determination of agronomic traits of ginseng fruit and seed

On August 10, 2020, ginseng fruits were collected, rubbed, and washed to obtain ginseng seeds. Twenty ginseng fruits and thirty ginseng seeds were detected in each treatment. The agronomic traits of fruit and seed determined in the present study were as follows: fruit weight, fruit grain weight, fruit grain number, fruit grain length, fruit grain width, fruit grain thickness, seeds weighing a hundred grains, seed length, seed width, seed thickness.

Determination of emergence and survival of ginseng plants

From June 15 to September 28, 2020, the emergence number of ginseng plants was counted every 15 days for a total of 8 times. The survival rate of ginseng plants was calculated according to the equation SR = SN/PN × 100%, where SR was the survival rate of ginseng plants, PN was the number of ginseng seedlings planted, and SN was the survival number of ginseng plants (H. Zhang et al., 2018).

Determination of the content of monomer ginsenosides and total ginsenosides

HPLC (high-performance liquid chromatography) analysis in the Chinese Pharmacopeia (Commission CP, 2015) was used. The analysis of root monomer ginsenoside contents followed the modified protocol of Zhang et al. (2013). Five dried ginseng roots from each treatment were mixed, ground using a mill (IKA All, Germany), and passed through sieves (60 mesh). Accurately weighed 0.1000 g ginseng root powder was ultrasonically extracted for two h with 10 mL 70% methanol. Solutions were filtered through a 0.2 μm membrane. The HPLC method was developed using a reversed-phase C18 column (100 mm × 2.1 mm, inner diameter 1.7 mm, Acquity UPLC BEH; Waters, Milford, MA, U.S.A.). Acetonitrile and water (containing 1 mL 85% phosphoric acid per liter) were used as mobile phases A and B, respectively. A gradient elution procedure was used as follows:
0–4.81 min, A 19%–19%, B 81%–81%;
4.81–7.31 min, A 19.0%–21.0%, B 81%–79%;
7.31–10.31 min, A 21.0%–28.0%, B 79%–72%;
10.31–16.31 min, A 28.0%–31.0%, B 72%–69%;
16.31–21.31 min, A 31.0%–38.5%, B 69%–61.5%;
21.31–22.00 min, A 38.5%–90.0%, B 61.5%–10%;
22.00–25.00 min, A 90.0%–90.0%, B 10%–10%;
25.00–25.50 min, A 90.0%–19.0%, B 10%–79%;
25.50–27.50 min, A 19.00%–19.0%, B 79%–79%.

The injection volume was two μL, and the flow rate was 0.4 mL min^{-1}. The column temperature was set at 45°C, and the measurement of U.V. absorbance was at 203 nm. The reference standards of Chikusetsu saponin IVa, notoginsenoside R_1, and ten monomer ginsenosides (Rg_1, Re, Rf, Rg_2, Rb_1, Ro, Rc, Rb_2, Rb_3, and Rd) were purchased from the National Institute for the Control of Pharmaceutical and Biological Products (Beijing, China).

Table 1. Effects of soil moisture on the agronomic traits of ginseng roots and aboveground organs.

	0.4 FC	0.6 FC	0.8 FC	1.0 FC
Root fresh weight (g)	5.384±0.88b	7.254±1.9b	10.944±1.54a	10.054±1.95a
Root dry weight (g)	1.558±0.25b	2.052±0.53b	2.996±0.42a	2.690±0.51a
Root length (cm)	27.4±3.49a	27.4±5.06a	27.5±3.64a	19.6±2.44b
Fibrous root length (cm)	20.1±5.62a	16.6±3.07ab	19.0±3.62a	11.4±1.42b
Root diameter (mm)	12.40±1.90a	12.64±0.43a	13.84±0.89a	14.22±1.55a
Bud length (mm)	10.39±1.28b	11.08±1.4ab	11.83±0.81ab	12.52±0.81a
Bud width (mm)	5.54±0.39b	5.9±0.94ab	6.60±0.58a	6.41±0.43ab
Aboveground dry weight (g)	0.545±0.08c	0.701±0.03b	1.221±0.12a	1.138±0.06a
Shoot height (cm)	18.0±2.26b	19.1±2.82ab	21.2±2.64a	23.3±1.93a
Stem diameter (mm)	3.94±0.71a	4.15±0.84a	4.28±0.30a	4.47±0.41a
Petiole length (cm)	3.7±0.12c	4.6±0.74b	5.7±0.28a	5.1±0.49ab
Leaf area (mm^2)	1,359.5±233.27c	1,724.32±171.24b	2,476.62±277.28a	2,332.00±376.34a

Different lowercase letters indicate significant difference. FC represents the field capacity of water in soil (29.38%).

The methods of total ginsenosides content measurement in the Chinese Pharmacopeia (Commission CP, 2015) were used. The content of total ginsenosides was determined by the single-point external standard method (Ginsenoside Re). The optical density was recorded at 544 nm by spectrophotometry.

Ginsenoside production was calculated according to the equation GP = DW × GC. Where GP is the ginsenoside production per ginseng root, DW is the dry weight of each root ginseng, and GC is the ginsenoside content of each treatment.

Statistical methods

Comparisons of the means used the least significant difference (LSD) at $P \leq 0.05$. All statistical analyses were performed using SAS v. 9.2 (SAS Institute, Cary, NC, U.S.A.).

Results

Effects of soil moisture on the agronomic traits of ginseng roots and aboveground organs

After nearly five months of growth, the agronomic traits of ginseng roots and aboveground organs under different water conditions showed significant differences. Generally, the 0.8 FC treatment showed the best results, followed by 1.0 FC, 0.6 FC, and finally 0.4 FC. The fresh root weight, root dry weight, aboveground dry weight, petiole length, and leaf area of ginseng increased with increasing soil moisture up to 0.80 FC and then decreased after that. These agronomic traits were significantly higher in the 0.8 FC and 1.0 FC treatments than in the other treatments ($P < 0.05$). Root diameter, bud length, shoot height, and stem diameter increased with soil moisture up to 1.0 FC. While root length and fibrous root length of 1.0 FC treatment were lower than the other treatments (Table 1).

The correlation analysis results of soil moisture and agronomic traits of root and aboveground organs of ginseng are shown in Supplemental Table S1. Soil moisture was negatively correlated with root length ($r = -0.77$) and fibrous root length ($r = -0.79$), but was positively correlated with the other agronomic traits, and among the other agronomic traits, root diameter ($r = 0.97$, $p < 0.05$), bud length ($r = 1.00$, $p < 0.01$), shoot height ($r = 0.99$, $p < 0.01$) and stem diameter ($r = 0.99$, $p < 0.01$) were significantly positively correlated with soil moisture. This indicated that soil moisture has certain effects on the growth of ginseng plant and root. Soil moisture was positively correlated with the most agronomic characters of root and aboveground organs of ginseng, except for root length and fibrous root length, indicating that soil moisture promoted the growth of ginseng plant and root, but inhibited the elongation of ginseng roots.

As shown in Figure 1, the root type of ginseng treated with 0.8 FC was larger, the bud was more significant, and the root bark was whiter. Some fibrous roots of 0.4 FC and 0.6 FC treatments became dry. The root type of ginseng treated with 1.0 FC was shorter and thicker, the bud was also more significant, and some of the roots were infected with red skin disease, with some red patches on the fibrous roots. Through observation, it was found that the taproot lengths in 4 treatments were not very different, and the root whole lengths and fibrous root lengths in 0.4 FC, 0.6 FC and 0.8 FC treat-

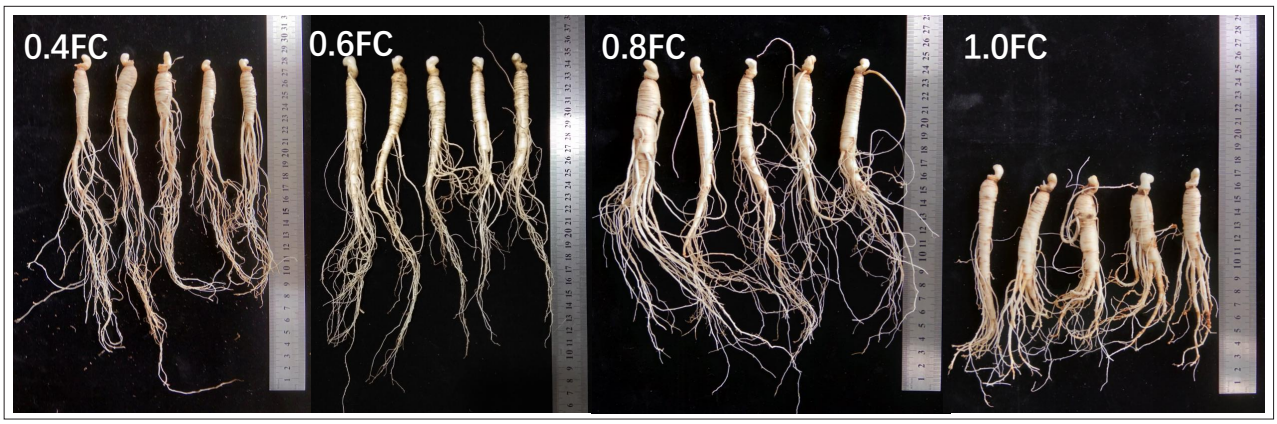


Figure 1. Ginseng roots treated with different soil moisture levels (after five months of growth).

Table 2. Effects of soil moisture on the agronomic traits of ginseng fruit and seeds.

	0.4 FC	0.6 FC	0.8 FC	1.0 FC
Fruit weight (g)	1.546±0.32b	2.314±0.77b	4.867±1.58a	4.602±1.90a
Fruit grain weight (g)	0.121±0.02d	0.151±0.03c	0.193±0.03b	0.211±0.05a
Fruit grain number	11.5±2.78b	14.1±5.11b	24.1±8.50a	21.1±8.99a
Fruit grain of length (mm)	6.29±0.46c	7.08±0.32b	7.86±0.50a	7.91±0.61a
Fruit grain of width (mm)	9.43±0.40c	10.55±0.43b	11.44±0.80a	11.37±0.81a
Fruit grain of thickness (mm)	4.54±0.64c	5.76±0.50b	6.74±0.52a	6.85±0.63a
Seeds weight a hundred grains (g)	8.402±0.25c	8.917±0.24b	10.420±0.12a	10.491±0.35a
Seed of length (mm)	5.27±0.33c	5.44±0.32c	5.76±0.32b	5.95±0.36a
Seed of width (mm)	4.22±0.31c	4.47±0.25b	4.69±0.29b	4.91±0.31a
Seed thickness (mm)	2.59±0.23c	2.76±0.23b	2.99±0.31a	2.91±0.25a

Different lowercase letters indicate significant difference (*n* of fruits = 20, *n* of seeds = 30, $p < 0.05$). FC represents the field capacity of water in soil (29.38%).

ments were also not significantly different, while the root whole lengths and fibrous root lengths in the 1.0 FC treatment were significantly shorter than the other treatments. The results showed that the high soil moisture treatment made the ginseng fibrous root shorter and then the whole ginseng root shorter.

These results suggest that adequate water was beneficial to the growth of ginseng roots and ground parts. Drought prevented ginseng plant growth and dry matter accumulation; the more severe drought stress was, the more negative the effects. Although beneficial to ginseng plant growth and the accumulation of dry matter in the roots, excessive water made the roots shorter and thicker, and more prone to red skin disorder.

Effects of soil moisture on the agronomic traits of ginseng fruit and seeds

The agronomic traits of ginseng fruit and seeds of 0.8 FC and 1.0 FC treatments showed better results. Fruit weight, fruit grain number, fruit grain width, and seed thickness increased with increasing soil moisture up to 0.8 FC and then decreased after that; these indices were significantly higher in the 0.8 FC and 1.0 FC treatments than in other treatments ($P<0.05$). Fruit grain weight, fruit grain length, fruit grain thickness, seeds weight a hundred grains, seed length, and seed width increased with soil moisture up to 1.0 FC (Table 2).

The correlation analysis results of soil moisture and agronomic traits of fruit and seed of ginseng are shown in Supplemental Table S2. Soil moisture was positively correlated with all the agronomic traits of fruit and seed of ginseng, and was significantly positively correlated with fruit grain weight ($r = 0.99$, $p < 0.01$), fruit grain of thickness ($r = 0.95$, $p < 0.05$), seeds weight a hundred grains ($r = 0.95$, $p < 0.05$), seed of length ($r = 0.99$, $p < 0.01$) and seed width ($r = 1.00$, $p < 0.01$). This indicated that soil moisture promoted the growth of fruit and seed.

As shown in Figure 2, ginsengs treated with 0.8 FC and 1.0 FC had plump fruits, larger fruit grains, more fruit grains, and larger seeds. The results showed that higher soil moisture was beneficial to the growth of ginseng fruit and seeds, and the characteristics and quantity of fruits and seeds increased. At the same time, drought hindered the development of fruits and seeds and reduced the weight, size, and amount of fruits and seeds.

Dynamic changes in the survival rate of ginseng seedlings under different soil moisture conditions during the growth period

The survival rate of ginseng seedlings gradually decreased for all treatments over time. The rate of decrease was slow from June 15 to July 30 (flowering stage to green fruiting stage) and then fast from July 30 to September 28 (red fruiting stage to wilt stage). The survival rate in 0.8 FC and 1.0 FC treatments were higher than that in 0.4 FC and 0.6 FC treatments during the whole growth period, and were significantly higher than that in 0.4 FC and 0.6 FC treatments from July 30 to September 28. On September 28, the survival rate of 0.4 FC, 0.6 FC, 0.8 FC and 1.0 FC treatments were

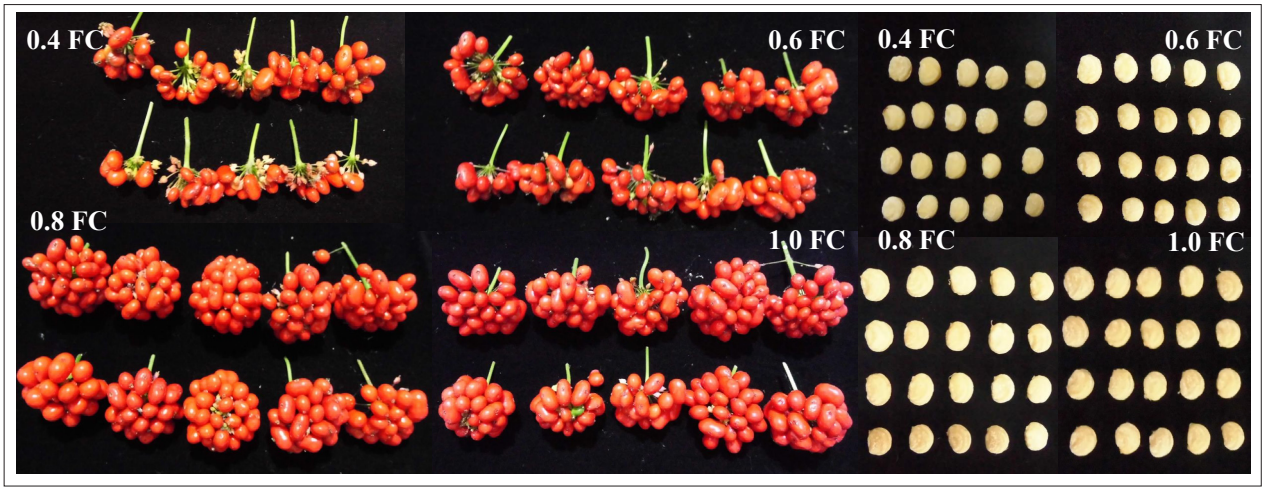


Figure 2. Ginseng fruits and seeds treated with different soil moisture levels.

5.6%, 13.75%, 71.25% and 68.13%, respectively, ranked as follows: 0.8 FC >1.0 FC >0.6 FC >0.4 FC (Figure 3A).

As shown in Figure 4, on August 10 and September 25, there were more seedlings under 0.8 FC and 1.0 FC treatments than the seedlings in 0.4 FC and 0.6 FC treatments. Especially on September 25, under the 0.4 FC and 0.6 FC treatments, most ginseng leaves turned yellow, and seedlings shriveled, while under the 0.8 FC and 1.0 FC treatments, most of the ginseng aboveground parts grew well, and the leaves remained green. The results indicated that drought stress accelerated ginseng seedling withering after fruit ripening, and the more severe the drought stress was, the faster the ginseng seedling withered.

Dynamic changes in the aboveground dry weight of ginseng under different soil moisture conditions during the growth period

As shown in Figure 3B, the aboveground dry weight of ginseng increased gradually over time from June 15 to July 30 (flowering stage to green fruiting stage) and then decreased after that. From June 15 to 30, the aboveground dry weight of ginseng ranked as follows: 1.0 FC> 0.8 FC> 0.6 FC> 0.4 FC, and from July 15 to September 28, ranked as follows: 0.8 FC> 1.0 FC> 0.6 FC> 0.4 FC.

This study showed that during the ginseng green fruiting stage, the aboveground dry weight of ginseng increased continuously, and higher soil moisture was beneficial to the accumulation of dry matter. At the same time, drought stress hindered the accumulation of dry matter. The more severe drought stress was, the more adverse dry matter accumulation. During the root growth and wilt stage (August 10 to September 28), the aboveground dry weight of ginseng continuously decreased, and drought stress accelerated the decline in dry matter.

Dynamic changes in the chlorophyll content in ginseng leaves under different soil moisture conditions during the growth period

The chlorophyll content in ginseng leaves was represented by the SPAD value measured by a chlorophyll meter.

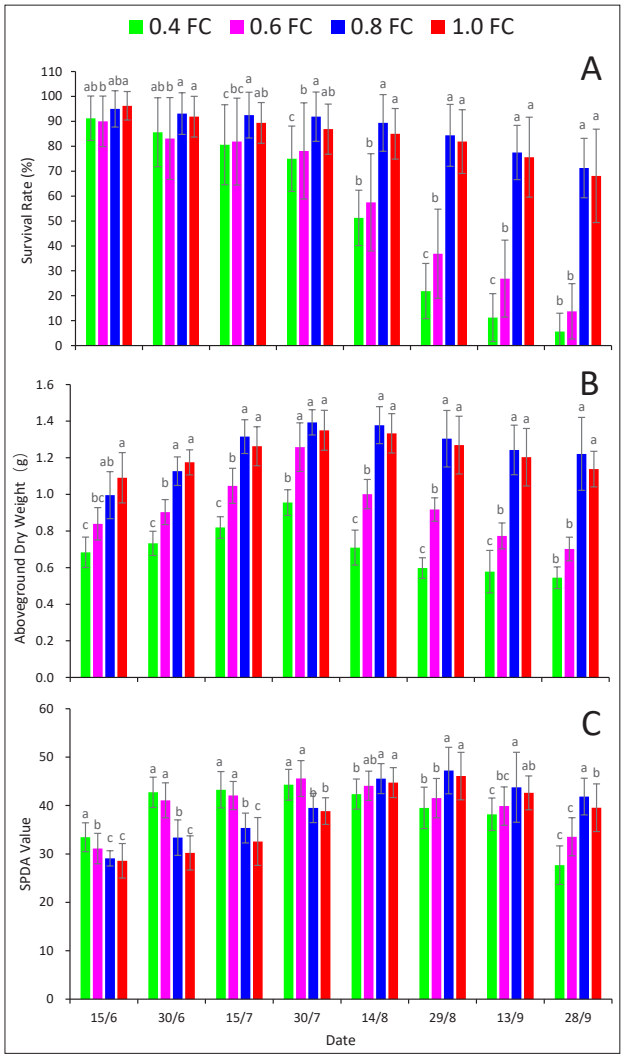


Figure 3. Dynamic changes in the survival rate of ginseng seedlings (A), aboveground dry weight (B), SPAD value (C) of ginseng under different soil moisture conditions during the growth period.



Figure 4. Ginseng seedlings of different soil water treatments on August 10 and September 25.

Table 3. Effects of soil moisture on the production of ginsenoside and total ginsenosides.

	0.4 FC	0.6 FC	0.8 FC	1.0 FC
R_1 content (mg)	0.451±0.07c	0.369±0.09c	0.778±0.10b	0.995±0.18a
Rb_1 content (mg)	6.370±1.00b	7.347±1.90b	10.845±1.50a	7.155±1.35b
Rb_2 content (mg)	3.208±0.50b	2.873±0.74b	6.021±0.83a	3.551±0.67b
Rb_3 content (mg)	0.763±0.12b	0.513±0.13c	1.018±0.14a	0.645±0.12bc
Rc content (mg)	3.084±0.48b	2.914±0.75b	5.243±0.72a	3.066±0.58b
Rd content (mg)	1.448±0.22b	1.600±0.41b	3.475±0.48a	1.641±0.31b
Re content (mg)	5.965±0.94c	8.373±2.17bc	12.253±1.69a	9.361±1.77b
Rf content (mg)	1.479±0.23b	1.518±0.39b	2.666±0.36a	1.156±0.21b
Rg_1 content (mg)	5.077±0.80b	5.254±1.36b	8.298±1.14a	4.008±0.76b
Rg_2 content (mg)	0.576±0.09b	0.882±0.22b	1.318±0.18a	0.941±0.17b
Ro content (mg)	2.710±0.42c	3.181±0.82c	6.351±0.87a	4.842±0.91b
IV a content (mg)	0.280±0.04b	0.328±0.08b	0.629±0.08a	0.538±0.10a
Total saponins content (mg)	97.552±15.42c	115.734±29.99bc	172.839±23.94a	142.096±26.95ab

Different lowercase letters indicate significant difference ($n = 5$, $p < 0.05$). FC represents the field capacity of water in soil (29.38%).

The chlorophyll content of 0.4 FC and 0.6 FC treatments increased gradually from June 15 to July 30 (flowering stage to green fruiting stage) and then decreased rapidly. The chlorophyll content of 0.8 FC and 1.0 FC treatments increased gradually from June 15 to August 29 and then decreased rapidly. On September 28, chlorophyll content of 0.4 FC, 0.6 FC, 0.8 FC and 1.0 FC treatments ranked as follows: 0.8 FC> 1.0 FC> 0.6 FC> 0.4 FC (Figure 3C). The results showed that after ginseng fruit ripening, sufficient water delayed the decline in chlorophyll content, while water deficit accelerated the rapid decline in chlorophyll content.

Effects of soil moisture on the content of monomer ginsenosides and total ginsenosides in dried ginseng roots

As shown in Figure 5, the contents of ginsenosides monomer Rb_1, Rb_2, Rb_3, Rc, Rf, Rg_1 and total ginsenosides for the four soil moisture treatments ranked as follows: 0.4 FC> 0.8 FC> 0.6 FC> 1.0 FC. Total ginsenosides content in the 0.4 FC treatment was 1.11, 1.09 and 1.19 times of that in 0.6 FC, 0.8 FC and 1.0 FC treatment, respectively. The contents of monomer ginsenosides Rd, Re, Ro and IVa in the 0.8 FC treatment were higher than other treatments. The monomer ginsenoside Rd content in the 0.8 FC treatment was 1.24, 1.48, and 1.91 times of that in 0.4 FC, 0.6 FC, and 1.0 FC treatment, respectively. Notoginsenoside R_1 content in the 1.0 FC treatment was higher than that in the other treatments and was 1.28, 2.10, and 1.43 times of that in 0.4 FC, 0.6 FC, and 0.8 FC treatment, respectively (Figure 5).

The correlation analysis results of soil moisture, monomer ginsenosides and total ginsenosides in ginseng roots are shown in Supplemental Table S3. Soil moisture was positively correlated with monomer ginsenosides R_1 ($r = 0.52$), Ro ($r = 0.41$) and IVa ($r = 0.67$), but was negatively correlated with the other monomer ginsenosides and total ginsenosides. This indicated that soil moisture promoted the accumulation of monomer ginsenosides R_1, Ro and IVa, but hindered the accumulation of the other monomer ginsenosides and total ginsenosides.

0.4 FC treatment was beneficial to accumulating monomer ginsenosides Rb_1, Rb_2, Rb_3, Rc, Rf, and Rg_1 and total ginsenosides. 0.8 FC treatment was beneficial to the accumulation of monomer ginsenosides Rd, Re, and Ro, and 1.0 FC treatment was beneficial to notoginsenoside R_1.

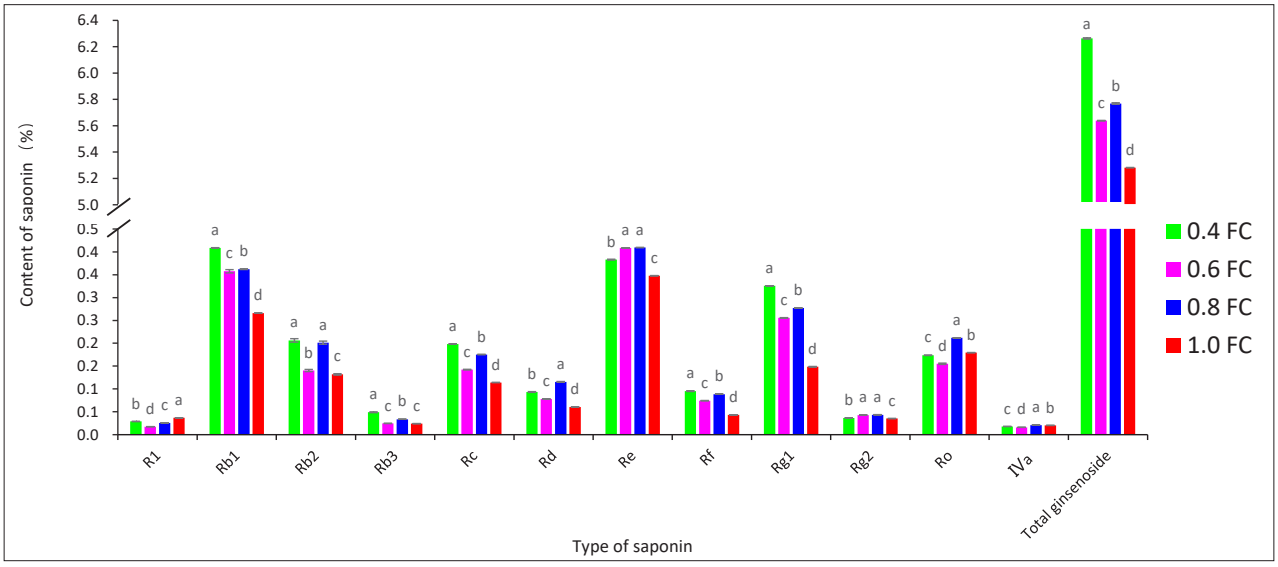


Figure 5. The contents of monomer ginsenosides and total ginsenosides in dried ginseng roots under different soil moisture conditions.

Effects of soil moisture on ginsenoside production

As shown in Table 3, the notoginsenoside R_1 production of each ginseng root in the 1.0 FC treatment was significantly higher than in other treatments, and was 2.21, 2.70 and 1.28 times of that in 0.4 FC, 0.6 FC and 0.8 FC treatment, respectively. The production of another 11 ginsenosides and total ginsenosides in each ginseng root increased with soil moisture to 0.80 FC and then decreased. These indices were higher in the 0.8 FC treatment than in other treatments (Table 3). This study showed that 1.0 FC was beneficial to the production of notoginsenoside R_1, while 0.8 FC was beneficial to the production of another 11 monomer ginsenosides and total ginsenosides.

Discussion

The growth of plants is affected by soil water, which affects plant morphogenesis and metabolism. Drought and waterlogging represent two main adverse environmental factors that severely harm plant development. Under drought conditions, the stomatal closure of leaves reduced the gas exchange rate, inhibited photosynthesis, and slowed dry matter accumulation (Wang et al., 2008). In contrast, excessive soil water conditions led to root hypoxia and reductions in metabolism, causing damage to plants and eventually the death of cells and tissues in non-adapted plants. Adaptation to long-term submergence is frequently associated with developmental changes such as root aerenchyma formation, petiole elongation, adventitious root development, and morphology (Ricoult et al., 2006). Studies on *P. notoginseng* have reported that extreme soil water conditions inhibit the growth of roots, stems, leaves, and flowers (Liao et al., 2017).

Effects of soil moisture on the aboveground organs of ginseng

Under the condition of water shortage, the lack of water absorption by plant roots affects the supply of nutrients and the growth of plant organs, inhibiting the plant height, canopy width, root growth and leaf size (Guo, 2012). In this study, soil moisture was positively correlated with the agronomic traits of the aboveground organs of ginseng (Supplemental Table S1), and the aboveground dry weight, plant height, stem diameter, petiole length, and leaf area of ginseng under the 0.8 FC and 1.0 FC treatments were higher than those plant parameters under the 0.4 FC and 0.6 FC treatments (Table 1). This result is partially consistent with Bao (2008), who found that the plant height and stem diameter of 1-year-old and 3-year-old ginseng increased with the increase of soil water content, and the 60~80% soil relative water content was beneficial to the growth of ginseng. This study indicated that drought stress harmed the development of ginseng plants, which may be due to drought stress in the early vegetative growth period, which slowed the growth of the plants by inhibiting cell expansion and division (Khan et al., 2021). From May 3 to June 15, ginseng experienced seedling and leaf development stages, which were the critical periods for determining the growth of ginseng aboveground (Yang, 2017). As 0.4 FC and 0.6 FC treatments began to reduce soil moisture during the two periods, the aboveground dry weight in 0.4 FC and 0.6 FC treatments were lower than that in 0.8 FC and 1.0 FC treatments from June 15 (Figure 3B), indicating that drought stress hindered the accumulation of dry matter in the aboveground part of ginseng. With the extension of treatment time, the aboveground dry weight in 4 treatments increased first and then decreased, and the decrease rate of 0.4 FC and 0.6 FC treatments were faster in the root growth stage and wilting stage (Figure 3B), which might demonstrate that drought stress accelerated the transfer of dry matter from ground to root and accelerated ginseng wilt.

In this study, the survival rate of ginseng decreased rapidly after fruit ripening; that is, ginseng quickly wilted. When the soil water condition was lower than 0.8 FC, ginseng seedlings wilted more than those treated with other treatments, and the more severe the drought stress, the faster the survival rate of ginseng decreased (Figure 3A). Park et al. (1982) found that the relative missing plant rate and defoliation of ginseng were significantly negatively correlated with soil water content. Similar results were also obtained by Ruiz-Sánchez et al. (2000), who found that partial defoliation has already been observed in young apricot plants under severe water stress conditions, which seems to be a tolerance mechanism. This study showed that drought accelerated ginseng wilt; the more severe the drought was, the faster the wilting speed, while sufficient soil moisture delayed ginseng wilt.

Leaf chlorophyll content is an important parameter that is frequently measured as an indicator of chloroplast development, photosynthetic capacity, leaf nitrogen content or general plant health. In this study, the chlorophyll content of ginseng treated with 0.4 FC and 0.6 FC showed an upward trend before fruit ripening and then decreased rapidly, while the chlorophyll content of ginseng treated with 0.8 FC and 1.0 FC showed an upward trend before wilting and then decreased rapidly (Figure 3C). Ling et al. (2011) found that with the senescence of Arabidopsis plants, leaves turned yellow, and chlorophyll content decreased gradually. Chlorophyll degradation brings the first visible sign of leaf senescence, which also occurs under unfavorable environmental conditions, including various biotic and abiotic stresses (Guo et al., 2021). The results showed that drought caused the chlorophyll content to decrease rapidly after fruit ripening, accelerated the degradation of chlorophyll, and led to premature senescence of ginseng.

Effects of soil moisture on fruit and seed of ginseng

Drought stress can affect the development of reproductive organs (including gametogenesis, fertilization, and embryogenesis) and grain development (Farooq et al., 2014). During the flowering and fruiting stage, plant growth is vigorous, and metabolism is enhanced (Wang et al., 2019). If drought stress occurs during the flowering or fruiting stage, it will result in abnormal development of plant reproductive organs, abortion of flowers, pods, and fruits, and ultimately affect crop yield (Pang et al., 2017). In the process of seed filling, water stress can slow down the grain filling speed, shorten the grain filling time, resulting in smaller grains (Sehgal et al., 2017). In this study, soil moisture was positively correlated with the agronomic traits of ginseng fruit and seed (Supplemental Table S2). The fruit grain number under 0.4 FC and 0.6 FC treatment were significantly fewer than that 0.8 FC treatment (Table 2; Figure 2), indicating drought stress caused some seed abortion and reduced seed setting rate of ginseng. The results showed that the size and weight of fruits and seeds under 0.4 FC and 0.6 FC treatments were significantly smaller than those under the 0.8 FC treatments. The results confirmed the finding of Park (1982b) that ginseng plants were sensitive to water deficit during fruition. Some indices of ginseng fruits and seeds treated with 1.0 FC were lower than the indices of ginseng fruits and seeds treated with 0.8 FC, but there were no significant differences; in contrast, some traits were significantly higher than 0.8 FC, such as seed weight, seed length, and seed width (Table 2).

This study indicated that drought stress hindered the growth of ginseng seeds and fruits. Therefore, ginseng plants used for seed production must ensure adequate soil moisture during the flowering and fruiting stages to improve the seed setting rate and seed quality and promote large fruit pulp and full-grain.

Effects of soil moisture on ginseng roots

In this study, soil moisture was positively correlated with the agronomic traits (except for root length and fibrous root length) of ginseng root (Supplemental Table S1). Both fresh and dry root weights of 0.4 FC and 0.6 FC treatments were significantly lower than those of 0.8 FC and 1.0 FC treatments. Both fresh and dry root weights in the 1.0 FC treatment were lower than the fresh and dry root weights in the 0.8 FC treatment, but there was no significant difference (Table 1). This finding is partially consistent with the finding of Gao (2019), who reported that 80% soil relative water content significantly promoted the growth of ginseng root, while 40% soil relative water content inhibited the growth of ginseng root. The results showed that drought stress hindered the accumulation of dry matter in ginseng roots, which may be because drought stress made the ginseng plants smaller and caused premature senescence, which seriously inhibited photosynthesis and organic matter production.

Ginseng bud, that is, ginseng overwintering bud is located on the root top side, and the well-developed bud is wrapped by three translucent scales in the production and cultivation of ginseng. The bud quality is closely related to the growth, development, flowering and fruit of ginseng in the next year (Ji et al., 2009). The buds grew rapidly with the rapid growth of ginseng roots, and when the aboveground plants were close to wilting, the buds had grown to average size. On September 28, the bud length and bud width of 0.8 FC and 1.0 FC treatments were higher than the other treatments' bud length and bud width (Table 1), indicating that adequate soil moisture was beneficial to ginseng bud growth and the development of ginseng in the next year.

When plants are affected by external factors, their appearance often changes in order to adapt to such changes (Ma et al., 2021). By observing the appearance of ginseng roots, the ginseng roots of 1.0 FC treatment were found to be short and thick, and parts of the ginseng fibrous roots had some red patches, indicating that excessive water increased the probability of ginseng infection with red skin disease. Wang (2016) found that when the soil moisture increased to 90% of the soil field capacity, the incidence of ginseng root erythroderma was higher, and the ginseng root was short and thick. This result is partially consistent with previous studies showing that high soil moisture and wet and compact soil conditions with poor soil permeability and ventilation promote the incidence and development of red skin disease (Lee et al., 2009, 2012; Liu et al., 2014).

Effects of soil moisture on content and production of ginsenoside

In contrast to the general reductions in growth and biomass gain, the concentrations of secondary metabolites were strongly enhanced in drought stressed plants (Kleinwächter et al., 2015). Abiotic stresses influence ginsenoside content, and proper management of abiotic stresses can promote ginsenoside content (Eo et al., 2018). Additionally, control of individual ginsenoside content may be needed because of the demand for specific pharmacological effects, such as monomer ginsenoside Rg_1, which has a pharmacological cardioprotective effect *in vivo* (Zhu et al., 2009). In this study, soil moisture was negatively correlated with monomer ginsenosides and total ginsenosides (except for monomer ginsenosides R_1, Ro and IVa) of ginseng (Supplemental Table S3). 0.8 FC treatment (adequate water supply) promoted the accumulation of monomer ginsenosides Rd, Re, and Ro. However, 0.4 FC (severe drought) promoted the accumulation of monomer ginsenosides Rb_1, Rb_2, Rb_3, Rc, Rf, Rg_1, and total ginsenosides. This result is partially consistent with previous works reported by Lim et al. (2006), Lee and Mudge (2013b) and Zhang et al. (2018) that soil moisture was negatively correlated with most of the individual ginsenosides, and suitable drought conditions could improve the biosynthesis of ginsenosides. While 1.0 FC (excessive water) treatment promoted the accumulation of notoginsenoside R_1, except for monomer ginsenosides R_1, Rg_2, Ro, and IVa, and the contents of the other seven monomer ginsenosides and total ginsenosides were all lower than the contents of the other seven ginsenosides and total ginsenosides for the other treatments. This result is partially consistent with a previous study reporting that high moisture had a negative effect on total ginsenoside (Lee et al., 2012).

Ginsenoside production was used to calculate the ginsenoside content in each ginseng root by combining the root's dry weight with the ginsenoside content. Ginsenoside production can be used to comprehensively analyze the effect of soil moisture on ginsenoside biosynthesis. The results showed that the production of 12 monomer ginsenoside ginsenosides and total ginsenosides in 0.4 FC and 0.6 FC treatments were significantly lower than those in 0.8 FC treatment. This result is partially consistent with a previous study which found that longer drought phases led to marked decreases in the overall contents of relevant natural products due to greater reductions in growth (Kleinwächter et al., 2015). The production of 11 monomer ginsenosides and total ginsenosides except for notoginsenoside R_1 in 1.0 FC treatment was lower than the production of those in 0.8 FC treatment. The results indicated that 0.8 FC (adequate water supply) was beneficial to ginsenoside production.

Conclusions

This study found that soil moisture impacted the growth of shoots, fruits, and seeds of ginseng. Water deficit (0.4 FC and 0.6 FC) stunted the growth of ginseng plants, fruit, and seeds and induced premature senescence. Adequate soil moisture (0.8 FC) increased the growth of ginseng plants, promoted large fruit pulp and larger seeds, and delayed the wilting of ginseng plants. Soil moisture affected root weight and ginsenoside production. Ginsenoside production and root weight could be promoted simultaneously under adequate soil moisture (0.8 FC). It led to a tradeoff between biomass and ginsenoside production. In contrast, severe drought (0.4 FC) increased some ginsenoside content but significantly reduced the yield and ultimately seriously affected ginsenoside production. Although excessive moisture (1.0 FC) had little effect on the growth and yield of ginseng, excessive moisture reduced the content of some ginsenosides and total ginsenosides, the ginseng root was short and thick, and some ginseng had a red skin disease, thus reducing the quality of ginseng. Therefore, 0.8 FC was the most suitable soil moisture for ginseng growth and ginsenoside production.

These results provide vital information that can guide a suitable irrigation management program that may be applied to intensive ginseng production systems for better

quality and higher ginseng root production. Soil moisture controls the production of certain monomeric ginsenosides and may seriously impact ginseng commerce and its future role in public health.

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Supplemental Information

Supplemental Information – Table S1. Correlation analysis between soil moisture and agronomic traits of root and aboveground organs of ginseng.

	Soil moisture	Root fresh weight	Root dry weight	Root length	Fibrous root length	Root diameter	Bud length	Bud width	Aboveground dry weight	Shoot height	Stem diameter	Petiole length	Leaf area
Soil moisture	1.00												
Root fresh weight	0.89	1.00											
Root dry weight	0.87	1.00**	1.00										
Root length	-0.77	-0.42	-0.37	1.00									
Fibrous root length	-0.79	-0.44	-0.39	0.93	1.00								
Root diameter	0.97*	0.93	0.91	-0.70	-0.64	1.00							
Bud length	1.00**	0.90	0.87	-0.76	-0.78	0.97*	1.00						
Bud width	0.89	1.00**	1.00**	-0.40	-0.42	0.92	0.89	1.00					
Aboveground dry weight	0.90	0.99**	0.99**	-0.47	-0.45	0.96*	0.91	0.99**	1.00				
Shoot height	0.99**	0.86	0.84	-0.82	-0.79	0.98*	0.99**	0.85	0.89	1.00			
Stem diameter	0.99**	0.88	0.85	-0.75	-0.81	0.93	0.99**	0.87	0.87	0.97	1.00		
Petiole length	0.81	0.98*	0.98*	-0.25	-0.33	0.83	0.81	0.98	0.95	0.75	0.81	1.00	
Leaf area	0.91	1.00**	1.00**	-0.45	-0.46	0.94	0.91	1.00**	1.00**	0.88	0.89	0.97*	1.00

Note: * indicates that the correlation is significant at 0.05 level; ** indicates correlation is significant at 0.01 level.

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Supplemental Information – Table S2. Correlation analysis between soil moisture and agronomic traits of fruit and seed of ginseng.

	Soil moisture	Fruit weight	Fruit grain weight	Fruit grain number	Fruit grain length	Fruit grain width	Fruit grain thickness	Seeds weight a hundred grains	Seed length	Seed width	Seed thickness
Soil moisture	1										
Fruit weight	0.92	1.00									
Fruit grain weight	0.99**	0.96*	1.00								
Fruit grain number	0.85	0.99**	0.92	1.00							
Fruit grain length	0.95*	0.97*	0.98*	0.94	1.00						
Fruit grain width	0.92	0.95	0.96*	0.93	1.00	1.00					
Fruit grain thickness	0.95*	0.95*	0.98*	0.93	1.00	1.00	1.00				
Seeds weight a hundred grains	0.95*	1.00**	0.98*	0.97*	0.95*	0.97*	0.96*	1.00			
Seed length	0.99**	0.95	0.99**	0.89	0.92	0.95*	0.95	0.97*	1.00		
Seed width	1.00**	0.92	0.99**	0.85	0.93	0.96*	0.96*	0.95	0.99**	1.00	
Seed thickness	0.87	0.97*	0.93	0.98*	0.98*	0.98*	0.97*	0.96*	0.89	0.88	1.00

Note: * indicates that the correlation is significant at 0.05 level; ** indicates correlation is significant at 0.01 level.

Supplemental Information – Table S3. Correlation analysis among soil moisture, monomer ginsenosides and total ginsenosides in ginseng roots.

	Soil moisture	R_1	Rb_1	Rb_2	Rb_3	Rc	Rd	Re	Rf	Rg_1	Rg_2	Ro	IVa	Total ginsenoside
Soil moisture	1.00													
R_1	0.52	1.00												
Rb_1	-0.92	-0.56	1.00											
Rb_2	-0.53	-0.07	0.78	1.00										
Rb_3	-0.73	0.08	0.78	0.86	1.00									
Rc	-0.77	-0.26	0.93	0.95*	0.91	1.00								
Rd	-0.34	-0.35	0.68	0.87	0.52	0.79	1.00							
Re	-0.47	-0.90	0.67	0.42	0.11	0.50	0.72	1.00						
Rf	-0.79	-0.52	0.97*	0.88	0.76	0.96*	0.84	0.27	1.00					
Rg_1	-0.88	-0.53	1.00**	0.83	0.80	0.95*	0.74	0.68	0.98*	1.00				
Rg_2	-0.09	-0.83	0.33	0.15	-0.26	0.16	0.58	0.92	0.42	0.34	1.00			
Ro	0.41	0.32	-0.03	0.55	0.16	0.27	0.67	0.11	0.20	0.54	0.20	1.00		
IVa	0.67	0.68	-0.41	0.24	-0.01	-0.06	0.27	0.33	0.20	0.33	0.17	0.89	1.00	
Total ginsenoside	-0.89	-0.27	0.95*	0.84	0.93	0.96*	0.60	0.41	0.91	0.95*	0.02	0.11	0.27	1.00

Note: * indicates that the correlation is significant at 0.05 level; ** indicates correlation is significant at 0.01 level.