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# Root architecture and nitrogen metabolism in roots of apple rootstock respond to exogenous glucose supply in low carbon soil

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**ABSTRACT**

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To investigate the response of root architecture and nitrogen metabolism of apple rootstock to glucose supply in low-carbon (C) soil, *Malus baccata* (L.) Borkh. in gravel soil was treated with glucose C equal to the soil microbial biomass carbon (MBC)-C value ($G_1$), five times the soil MBC value ($G_2$), or with no glucose (CK). The roots samples were harvested after treatments for 7, 15 and 30 days. The roots tended to become larger, more dichotomous and showed a larger link branching angle in $G_1$ and $G_2$ than in CK, especially in the $G_1$ treatment for 30 days. Plant height and biomass were increased by G1. Nitrate ($NO_3^-$-N) and nitrite ($NO_2^-$-N) contents were increased, but ammonium ($NH_4^+$-N) concentration was decreased in the roots treated with $G_1$ and $G_2$ in all treatment periods. Also, the activities and transcript levels of nitrate reductase, glutamine synthetase, glutamate dehydrogenase, glutamate synthase were generally increased in roots treated with glucose, especially under $G_1$. The activities of glutamic oxalacetic transaminases and glutamic-pyruvic transaminase were higher under $G_1$ than under either $G_2$ or CK. Exogenous carbon source that equals to the native MBC effectively regulated the root architecture and supported increasing nitrogen absorption and metabolism in plants growing under carbon-restricted conditions.

**Keywords**: external carbon source; nitrogen uptake and assimilation; root morphology and topology; transcript levels

In China apple orchards are often established on hills or in wastelands, which have poor parental material structure as well as low soil organic content and fertility. Addition of external carbon (C) source is an effective method to regulate root architecture and nutrient absorption, and consequently increases apple yield and quality. Previous studies showed that the root architecture is regulated by soil organic carbon (SOC) (Lastdrager et al. 2014). SOC has a significant positive correlation with soil microbial biomass carbon (MBC), and the amount of MBC is known to vary in different soil types. The amount of supplied carbon source was determined relative to the level of soil MBC. (1) When it is similar to soil MBC, it induces a positive priming effect (PE), promoting SOM decomposition, but microbial activity is not affected. (2) When it is 200–500% higher than soil MBC, the PE tends to be zero or even negative (Blagodatskaya and Kuzyakov 2008). Therefore, MBC is an important factor for identifying the optimal amount of exogenous carbon source to supply to low-C soil.

Previous studies demonstrated that glucose is a typical, abundant and low-molecular-weight substance that is involved in root development, elongation and nutrient cycles (Singh et al. 2014). Nitrogen is one of the essential mineral elements for plant growth and crop yield, nitrogen uptake is affected by the exogenous organic matter (Ruffel et al. 2014). Glucose generally promotes the assimilation and metabolism of nitrogen, and increases activity of enzymes (Iglesias-Bartolomé et al. 2004). Moreover, the reduction in sugar levels inhibits nitrate assimilation in plants (Matt et al. 2002). Glucose regulates the translocation of ammonium ($NH_4^+$-N) and nitrate ($NO_3^-$-N), as well

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as the expression of genes encoding nitrate reductase (NR) (Reda 2015). However, no information is available on the effect of different concentrations of exogenous glucose on root architecture and nitrogen metabolism or the expression of genes associated with nitrogen assimilation in apple rootstocks under low-C soil conditions.

The objectives of this study were to investigate the root architecture, nitrogen metabolism ($NH_4^+$-N, $NO_3^-$-N and $NO_2^-$-N content, enzymes and the transcriptional levels involved in nitrogen assimilation) of *Malus baccata* (L.) Borkh. seedlings exposed to glucose under low C soil conditions.

## MATERIAL AND METHODS

**Study area and plant cultivation**. In April 2016, 15 gravel soil samples (40 × 40 × 40 cm) were collected from apple orchards in the Xingcheng city (40°36'41.66''N, 120°43'56.32''E) in the Liaoning province of China. In this area, the altitude is 75 m a.s.l., average rainfall is 600 mm and average temperature is 8.7°C. The roots and visible plant residues were removed from the soil. The homogenized soil samples contained 13.06% clay, 16.58% silt and 70.36% sandy were sieved (< 5 mm). The soil chemical properties were as follows: $pH_{H_2O}$, 6.99; organic carbon ($C_{org}$), 4.52 g C/kg; MBC, 1.23 mg C/g; potentially available nitrogen (alkaline hydrolysing), 114.63 mg N/kg; available phosphorus (Olsen method), 6.47 mg P/kg; available potassium (ammonium acetate), 126.22 mg K/kg. One-year-old *Malus baccata* (L.) Borkh. seedlings with 7–8 leaves and similar size were transplanted to plastic pots (16 × 14 cm). One seedling was planted in each pot filled with 1 kg of homogenized soil.

**Experimental setup and plant sampling**. The study was conducted outdoors under a transparent rain shelter at the experimental field of the Shenyang Agricultural University, Shenyang, China from 15 April to 21 July 2016. The glucose treatments were conducted after the seedlings had been transplanted for 5 weeks. A total of 150 seedlings of similar size were selected for the experiment and divided into three groups. Within each group, 50 seedlings were treated with glucose C equal to the soil MBC value ($G_1$, 3.0 g/kg of glucose); 50 seedlings were treated with glucose C five times the soil MBC value ($G_2$, 15.0 g/kg glucose); and 50 seedlings were not treated with glucose (CK). The glucose was dissolved in 150 mL distilled water and the roots were irrigated with it once at the beginning of the treatments. Henceforth, all plants were supplied daily with water before harvest. After 7, 15 and 30 days of treatments, root samples were collected from 15 plants (five seedlings in each replication) from each treatment, which were wrapped with tinfoil and immediately frozen in liquid nitrogen. The frozen samples were milled to a fine powder with a ball mill (Retsch, Haan, Germany) precooled in liquid nitrogen and then stored at –80°C for further analysis. The remaining five plants from each treatment at the end of 30-day treatments were used to evaluate root architecture and biomass.

**Biomass and root architecture analysis**. The roots were cleaned, placed in a transparent tray (20 × 25 cm) with deionized water and scanned using an Epson Perfection V800 Photo scanner (Epson, Long Beach, USA), then digitized and measured by Winrhizo (Regent Instruments Inc., Quebec, Canada). The total root length, average root diameter, root volume and root surface were determined. The architecture traits, including Pe (external path length) is the sum of the number of links in all paths from each external link to the base link; link branching angle is the angle between the link and the extension of the preceding link; DBI is the dichotomous branching index, DBI = [Pe-min(Pe)]/[(max(Pe) – min(Pe)] and TI (Topological index) is the slope of the linear regression of log10 (Pe)/log10 (μ); Winrhizo recognizes all root endings as root tips (μ) and they were calculated as described by (Fitter 1987).

The plant height was measured with a meter rule. For dry weight measurements, the root and shoot tissues were oven-dried for 8 h at 80°C to constant weight.

**Measurement of $NO_3^-$-N, $NO_2^-$-N and $NH_4^+$-N concentrations**. The $NO_3^-$-N, $NO_2^-$-N and $NH_4^+$-N concentrations were measured by TU-1900UV-vis spectrophotometry (Purkinje, Beijing, China) at 410, 540 and 570 nm as described by Patterson et al. (2010), Ogawa et al. (1999) and Bräutigam et al. (2007), respectively.

**Activity of enzymes involved in nitrogen metabolism**. The activities of nitrate reductase and glutamine synthetase (GS) were measured by determining the absorbance at 540 nm as described by Högberg et al. (1986) and Yu and Zhang

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(2012), respectively. The activity of glutamate synthase (NADH-GOGAT) and glutamate dehydrogenase (NADH-GDH) were measured by monitoring the oxidation of NADH at 340 nm as described by Robinson et al. (1991) and Loulakakis and Roubelakis-Angelakis (1990), respectively. The activity of glutamic-oxaloacetic (GOT) and glutamic-pyruvic transaminase (GPT) were measured by determining the absorbance at 500 nm according to Bergmeyer and Bernt (1974). All absorbance was measured by TU-1900UV-vis spectrophotometry (Purkinje, Beijing, China).

**Quantitative real-time PCR (qRT-PCR) analysis**. Total RNA was isolated and purified as described by Chang et al. (1993). Quantitative PCR was tested by ABI 7500 (Life Technology, Applied Biosystems, Foster City, USA). β-actin was used as a reference gene. The relative expression of each gene was calculated using the $2^{-\Delta\Delta CT}$ method (Livaka and Schmittgen 2001).

**Statistical analysis**. All results were shown as means of three replicates with standard deviation. The mRNA expression level was set to 1 in the roots of the CK in 7 days. Significantly different means were separated at $P < 0.05$ by the Duncan's test. All analyses were performed using the SPSS (version 18.0, SPSS Inc., Chicago, USA).

## RESULTS AND DISCUSSION

**Effects of exogenous sugar on root architecture**. Glucose is the main monosaccharide in the physiological metabolism of plants, which regulates taproot length by controlling the apical meristematic zone (Yuan et al. 2014), and it induces changes in the root architecture. In our study, $G_1$ had the most positive effect on the root architecture of *M. baccata*, leading to significantly higher total length (59.2% higher), surface area (43.9% higher) and root volume (92.8% higher) than in CK, whereas $G_2$ led to an increase in root volume of only 45.7% (Figure 1a–c). Root length decreases with increasing soil particle size (Popova et al. 2016), and the longer root length indicates that exogenous glucose supply could alleviate many limitations to root development in gravel soil (Tracy et al. 2013). The increased total root length, root volume and root surface of *M. baccata* treated with $G_1$ may be driven by the quick growth of plants and consequent nutrient exhaustion in the rhizosphere or the intense competition among the roots, with exogenous carbon source supply (Blagodatskaya and Kuzyakov 2008). In this study, DBI in $G_1$ and $G_2$ was significantly lower by 45% and 50% than that in the CK, respectively, which

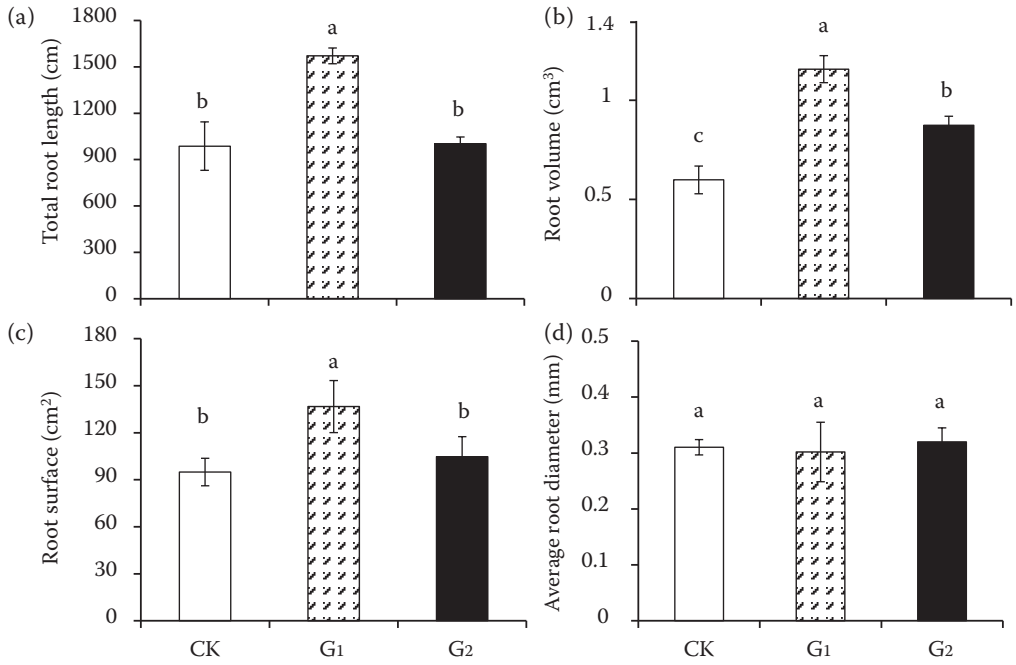


Figure 1. (a) The total root length; (b) root volume; (c) root surface and (d) average root diameter of *Malus baccata* (L.) Borkh. as affected by glucose supply in gravel soil for 30 days. Data indicate means ± standard deviations ($n = 5$). Different letters on the bars indicate significant differences between treatments at $P < 0.05$. CK – absence of glucose; $G_1$ – 3 g/kg; $G_2$ – 15 g/kg glucose

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Table 1. The growth and root architecture of *Malus baccata* (L.) Borkh. as affected by different glucose levels in gravel soil

| Treatment | Number of links | Number of tips | Pe | Link length (cm) | Link branching angle | DBI | TI | Height (cm) | Root biomass | Shoot biomass |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | (g) | |
| CK | 7877 ± 172$^{c}$ | 2150 ± 18$^{b}$ | 69 266 ± 5157$^{b}$ | 0.13 ± 0.03$^{a}$ | 43.56 ± 0.69$^{c}$ | 0.057 ± 0.003$^{a}$ | 1.26 ± 0.02$^{a}$ | 29.64 ± 1.52$^{c}$ | 1.60 ± 0.13$^{b}$ | 2.79 ± 0.31$^{b}$ |
| $G_1$ | 14657 ± 72$^{a}$ | 3179 ± 107$^{a}$ | 119 171 ± 345$^{a}$ | 0.11 ± 0.01$^{b}$ | 55.46 ± 0.09$^{a}$ | 0.049 ± 0.002$^{b}$ | 1.14 ± 0.04$^{c}$ | 36.60 ± 1.85$^{a}$ | 1.84 ± 0.09$^{a}$ | 3.65 ± 0.21$^{a}$ |
| $G_2$ | 9842 ± 296$^{b}$ | 2359 ± 158$^{b}$ | 73 498 ± 2479$^{b}$ | 0.13 ± 0.01$^{a}$ | 50.97 ± 1.76$^{b}$ | 0.048 ± 0.001$^{b}$ | 1.20 ± 0.00$^{b}$ | 32.46 ± 2.00$^{b}$ | 1.73 ± 0.09$^{ab}$ | 2.93 ± 0.04$^{b}$ |

Data indicate means ± standard deviations ($n$ = 5). Different letters indicate significant differences between treatments at $P < 0.05$. Pe (External path length), the sum of the number of links in all paths from each external link to the base link. Link branching angle is the angle between the link and the extension of the preceding link. DBI (Dichotomous branching index), DBI = [Pe – min(Pe)]/[(max(Pe) – min(Pe)]. TI (Topological index) is the slope of the linear regression of $\log_{10}$(Pe) versus $\log_{10}$(μ), Winrhizo recognizes all root endings as root tips (μ). CK – no added glucose; $G_1$ – 3 g/kg glucose; $G_2$ – 15 g/kg glucose

means roots were more dichotomous and less herringbone-like under exogenous glucose, and benefited from acquiring diffusion-limited nutrients (Fitter 1987) thus inducing root and shoot biomass accumulated and increased plant height, especially under $G_1$. $G_2$ showed no marked effect on shoot biomass, compared with CK (Table 1). Changes in the root length and link branching angle could alter the root topological structure; they are the most critical components of the root architecture. Previous studies confirmed that glucose plays a key role in regulating the root architecture by accelerating the growth of the existing lateral roots and promoting the formation of new lateral roots (Roycewicz and Malamy 2012). The number of root tips, links and Pe were significantly promoted by $G_1$, the root angle was higher in $G_1$ and $G_2$ than in CK (Table 1). Singh et al. (2014) showed that glucose promoted deviation from vertical growth. The increased angle revealed

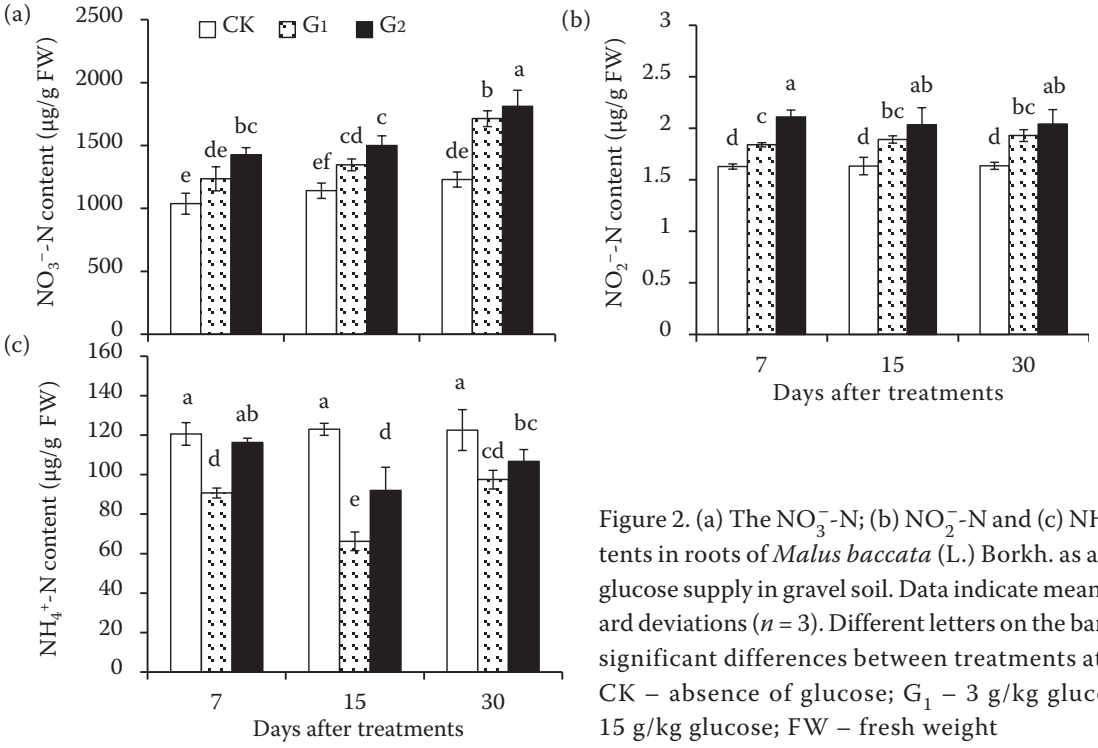


Figure 2. (a) The $NO_3^-$-N; (b) $NO_2^-$-N and (c) $NH_4^+$-N contents in roots of *Malus baccata* (L.) Borkh. as affected by glucose supply in gravel soil. Data indicate means ± standard deviations ($n$ = 3). Different letters on the bars indicate significant differences between treatments at $P < 0.05$. CK – absence of glucose; $G_1$ – 3 g/kg glucose; $G_2$ – 15 g/kg glucose; FW – fresh weight

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that the root fed with $G_1$ and $G_2$ might follow a horizontal growth pattern, thus improving their exploitation ability in order to maintain optimal water and nutrient uptake. Changes in root elongation, branching, and angle due to exogenous glucose supply may indicate that the root follows an exploratory growth strategy, and any shifts of the architecture aim at more efficient nutrient acquisition and effective exploration of larger soil volumes, especially under $G_1$ treatment.

**Effects of exogenous sugar on nitrogen metabolism of plant**. Nitrogen is a vital abundant inorganic nutrient in plants and its availability affects plant growth and development (Nacry et al. 2013). Exogenous glucose or sucrose affects the assimilation of nitrogen in plant tissues (Iglesias-Bartolomé et al. 2004). $NO_3^-$-N is generally used as the major nitrogen source for plants and its uptake is a highly energy-consuming process (Bloom 2015). Compared with CK, significant $NO_3^-$-N and $NO_2^-$-N concentrations were accumulated in $G_1$ and $G_2$ treatments (Figure 2). Meanwhile, exogenous glucose supply increased the root length and root surface area and also changed root angle (Table 1), improving the absorbance of potentially available N in the soil. Foyer et al. (2011) demonstrated that exogenous C supply promotes $NO_3^-$-N uptake and assimilation. $NO_3^-$-N is reduced to $NO_2^-$-N by NR, the NR activity in root under $G_1$ and $G_2$ treatments was significantly higher than CK at 7 days and 15 days, but no significant differences were found at 30 days (Figure 3). However, the $NH_4^+$-N concentrations in roots under $G_1$ and $G_2$ treatments were significantly decreased, especially under $G_1$ (Figure 2c), which was similar with Bargmann et al. (2014). Li et al. (2013) demonstrated that a higher supply of $NH_4^+$-N inhibits root growth and produces abnormal growth of lateral roots. In this work, a decreased $NH_4^+$-N and an increased $NO_3^-$-N concentration by exogenous glucose treatments also supported lateral root growth, as shown in Table 1.

The GS, NADH-GDH and NADH-GOGAT are three key enzymes in the GS/GOGAT cycle. The activity of NADH-GOGAT showed a decreased trend in all treatment times and was always significantly higher in $G_1$ and $G_2$ than in CK; the highest activity was found at 7 days under $G_1$ treatment. Overall, the external glucose supply can improve the

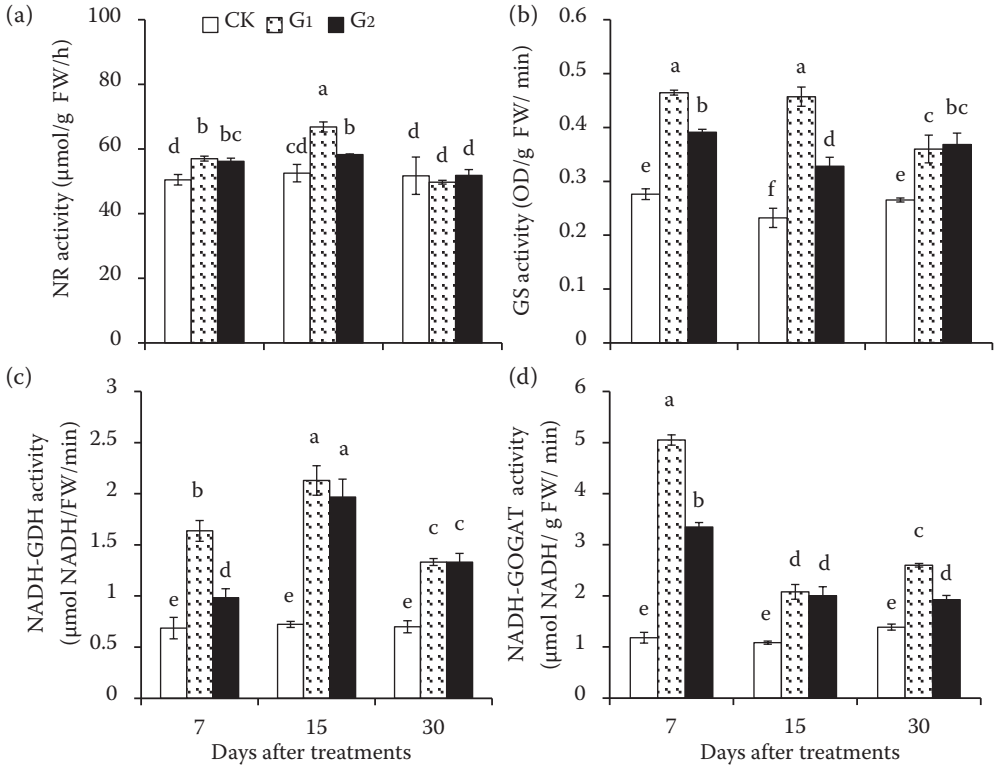


Figure 3. (a) Activities of nitrate reductase (NR); (b) glutamine synthetase (GS); (c) glutamate dehydrogenase (NADH-GDH) and (d) glutamate synthase (NADH-GOGAT) in roots of *Malus baccata* (L.) Borkh. as affected by glucose supply in gravel soils. Data indicate means ± standard deviations ($n$ = 3). Different letters on the bars indicate significant differences between treatments at $P < 0.05$. CK – absence of glucose; $G_1$ – 3 g/kg glucose; $G_2$ – 15 g/kg glucose

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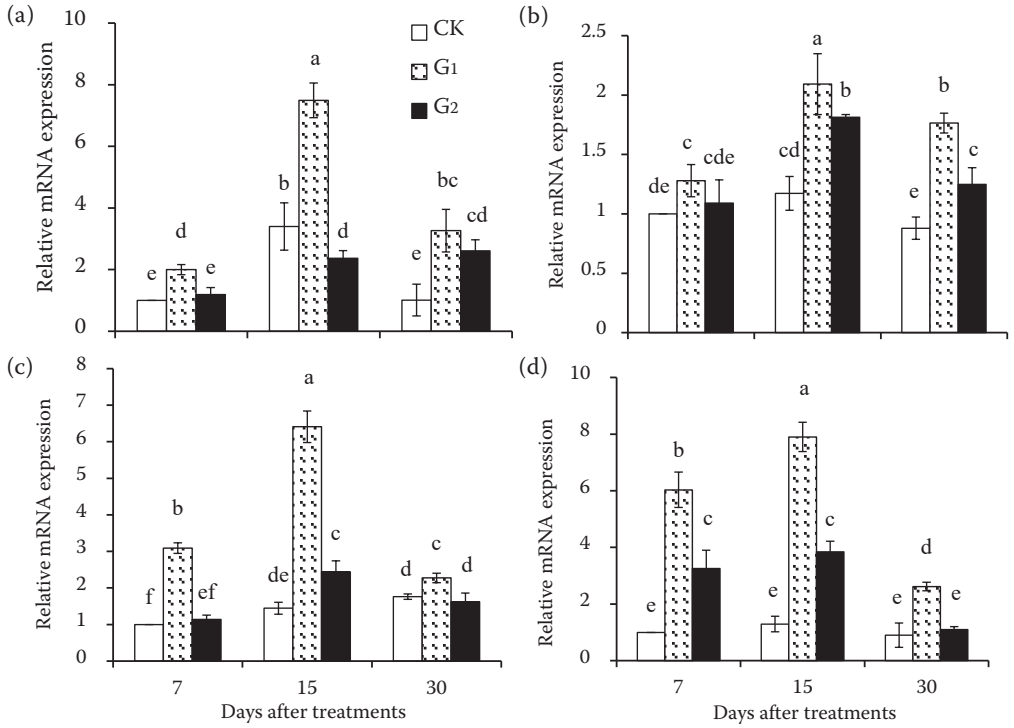


Figure 4. The relative expression of (a) nitrate reductase; (b) glutamine synthetase; (c) glutamate dehydrogenase, and (d) glutamate synthase involved in nitrogen metabolism in roots of *Malus baccata* (L.) Borkh. as affected by glucose supply in gravel soil. Data indicate means ± standard deviations ($n$ = 3). Different letters on the bars indicate significant differences between treatments at $P < 0.05$. CK – absence of glucose; $G_1$ – 3 g/kg glucose; $G_2$ – 15 g/kg glucose in soil

absorption and assimilation of nitrogen in root, which may be due to the increased activities of NR, GS, NADH-GDH and NADH-GOGAT (Figure 3), and upregulate the mRNA expression of relative genes in all treatment times, except NR activity in 30 days and mRNA expression in 15 days (Figure 4). These results were consistent with previous studies (Reda 2015). Coruzzi and Zhou (2001) reported that a small amount of C supply upregulated the expression of genes related to N metabolism; thus, $G_1$ treatments exhibited higher positive effects than $G_2$ treatment.

Glutamate can be further converted to aspartic acid or alanine by GOT or GPT. As shown in Figure 5, the activities of GPT and GOT were greatly

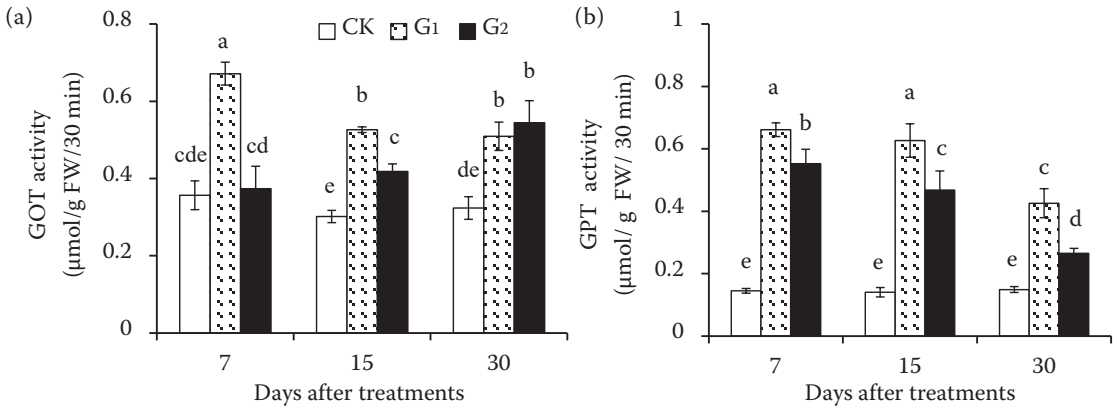


Figure 5. Activities of (a) glutamic oxaloacetic transaminase (GOT) and (b) glutamic-pyruvic transaminase (GPT) in roots of *Malus baccata* (L.) Borkh. as affected by glucose supply in gravel soil. Data indicate means ± standard deviations ($n$ = 3). Different letters on the bars indicate significant differences between treatments at $P < 0.05$. CK – absence of glucose; $G_1$ – 3 g/kg glucose; $G_2$ – 15 g/kg glucose; FW – fresh weight

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increased under $G_1$ and $G_2$, and $G_1$ had a stronger positive effect on the activities of GPT and GOT than $G_2$. Therefore, exogenous C supply to low C soils contributes to N assimilation due to the increased activities and mRNA expression of key enzymes, to maximize the absorption and assimilation of N and to be used for amino acid synthesis.

In summary, exogenous C supply in a concentration equal to MBC content was effective to promote the root architecture, improve nitrogen absorption and assimilation ability in root of *Malus baccata* (L.) Borkh. in gravel soil conditions.

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