Scientia Horticulturae 218 (2017) 125–131

Contents lists available at ScienceDirect

Scientia Horticulturae

journal homepage: www.elsevier.com/locate/scihorti

Distribution and redistribution of phosphorus forms in grapevines

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ARTICLE INFO

Article history:
Received 13 September 2016
Received in revised form 30 January 2017
Accepted 10 February 2017

Keywords:
Phosphate fertilizer
Chemical fractionation of P in the tissue
Vitis vinifera L.

ABSTRACT

Increased phosphorus (P) available in soil can modify the partitioning of P forms in annual and perennial organs of grapevines throughout the growing season. This study was to evaluate the distribution and redistribution of P forms in organs of grapevines grown in soils with different contents of available P. The study was conducted in two vineyards installed in the city of Santana do Livramento, state of Rio Grande do Sul (RS), in southern Brazil. The treatments were vineyard 1 (V1) with 11.8 mg kg^{-1} of available P in soil and vineyard 2 (V2) with 34.6 mg kg^{-1}. The cultivar of both vineyards is Tannat (*Vitis vinifera* L.) grafted on SO4 (*Vitis berlandieri* × *Vitis riparia*) rootstock. Plant density per hectare was 2525 (1.2 m × 3.2 m) on a spur pruned cordon system. The grapevines were uprooted and partitioned into roots, trunks, arms, spurs, new-year shoots, leaves and clusters (when present) at flowering (F), veraison (V), harvest (H) and dormancy (D). The organs were dried, prepared and subjected to chemical fractionation of P, to estimate fractions of total acid-soluble P (P_{ST}), acid-soluble inorganic P (P_{SI}), acid-soluble organic P (P_{SO}) (by difference between T_{SP} and P_{SI}), phospholipids P (P_{LIP}), P associated with RNA (P_{RNA}), P associated with DNA (P_{DNA}) and residual P (P_{RES}). P in grapevines of V1 and V2 accumulated mainly in the P_{SI} fraction in leaves and clusters, which was collected at F, V and H, and in P_{SO} fraction in roots, collected at D. Part of the root P_{SI} was redistributed at F to the leaves and clusters in vines of V1. Vines grown in V2 accumulated more P in P_{SO} form in roots and tended to redistribute less P_{SI} to the leaves and clusters after F. Grapevines accumulated P in roots, both in soils with low and high available P contents, and P was subsequently redistributed and accumulated in leaves and clusters in inorganic form.

1. Introduction

Phosphorus is one of the elements that most often limits agricultural productivity in the world. In the soil-plant system, P is characterized by having very low mobility in soil, because it is adsorbed strongly by iron and aluminum oxides of highly weathered soils and by forming complexes with Ca in calcareous soils (Bortoluzzi et al., 2015; Fink et al., 2014, 2016). However, it has high mobility within the plant and it is redistributed from one organ to another according to demand and availability of P in soil (Schachtman et al., 1998). In the face of a predicted imminent shortage of phosphate reserves in the middle of this century (Cordell et al., 2009), it is essential to improve understanding of the physiological and metabolic aspects of the use of P by plants in order to design strategies to improve the efficiency of P-fertilization.

Within plants such as grapevines (*Vitis vinifera* L.), P can be accumulated in organic forms such as metabolically active organic P in the cytoplasm (P_{SO}), phospholipids (P_{LIP}), P associated with RNA and DNA (P_{RNA} and P_{DNA}), phosphoproteins (P_{RES}) and in inorganic phosphorus (P_{SI}) form (Bieleski, 1973; Veneklaas et al., 2012).

It is believed that plants grown in soils with greater P availability tend to accumulate higher levels of P in organs in P_{SI} form, especially in annual organs, such as leaves, and in annual crops, in grains (Martinez et al., 2005; Lambers et al., 2011). The P_{LIP} fraction represents P contained primarily in cell membranes (Bieleski, 1973) and its increase typically happens because of the increase in com-

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http://dx.doi.org/10.1016/j.scienta.2017.02.023
0304-4238/

plexes of cell membranes, especially thylakoid at plant flowering (Thomas and Sadras, 2001), in response to increase in P_{SI} content (Reef et al., 2010; Veneklaas et al., 2012). P content in ribonucleic acids (P_{RNA} and P_{DNA}) usually differs among organs, tissues and cells, and is higher especially in expanding leaves, lower in adult leaves, and very low in senescent leaves (Suzuki et al., 2001; Niklas, 2006). Generally, P_{SO} content in annual organs such as leaves and fruit varies slightly with increasing availability of soil P (Lee and Ratcliffe, 1983). However, when cell division in these organs ceases, P may be redistributed and accumulated in perennial organs such as roots, the main nutrient reserve organ in fruit trees (Lima et al., 2011).

In adult grapevines, it is not sufficiently known if the increase in P content available in soil can actually change the distribution of P forms, such as P_{SI}, P_{SO}, P_{RNA} and P_{LIP}, in annual organs (leaves, new year shoots and clusters) and perennial organs (roots, trunks, arms and spurs) throughout the phenological stages. For example, if the amount of P forms in annual organs is high, P depletion within the plant is expected, especially if the soil does not possess P in sufficient quantities to meet plant demand. On the other hand, if P forms are primarily accumulated in reserve organs such as roots, they are expected to contribute to the growth of annual organs in the following cycle, thus decreasing the dependence of the plant on soil P. However, this dynamic redistribution of P forms from perennial to annual organs throughout phenological stages of adult grapevines at field level has rarely been studied. Therefore, this study aimed to evaluate the distribution and redistribution of P forms in grapevines grown in soil with different contents of available P.

2. Material and methods

2.1. Description of the experimental area

The study was conducted from August 2014 to March 2015 in two vineyards (V1 and V2) of the city of Santana do Livramento (Latitude 30° 49′ 8" S, Longitude 55° 27′ 3" W and altitude of 320 m), located in the Campanha Gaúcha region of Rio Grande do Sul (RS), southern Brazil. The soil of both vineyards is a Typic Hapludalf (Soil Survey Staff, 2006). The relief in both vineyards is slightly undulated with a 12% declivity. The physical and chemical characteristics of the both vineyard soils for the 0 – 20 cm layer are shown in **Supplementary material 1**. The climate is humid subtropical Cfa according to Köppen classification, which is characterized by mild temperatures and rain with little variation throughout the year. The average annual rainfall is approximately 1600 mm. The average temperature of the hottest month of the year (January) is 23.8° C and the average temperature of the coldest month (July) is 12.4° C. The annual sunshine is approximately 2500 h. Phenological stages, monthly average values of rainfall, temperature, humidity and sunshine observed during the study are shown in **Supplementary material 2**.

2.2. Treatments

The treatments were two vineyards with two contents of available P in soil (extracted by Mehlich-1). Soil in V1 had 11.8 mg P kg^{-1} (considered low in a soil with 15% clay) and V2 34.6 mg P kg^{-1} (considered high in a soil with 10% clay) (Committee on Soil Chemistry and Fertility, 2004). V1 was established in 2004 and V2 in 2003. The cultivar of both vineyards is Tannat (*Vitis vinifera* L.) grafted on SO4 (*Vitis berlandieri* × *Vitis riparia*) rootstock. Plant density per hectare was 2525 (1.2 m × 3.2 m) on a spur pruned cordon system. The experimental design was randomized blocks with three replications. Each replication was formed by five plants and the three central grapevines were evaluated. During the experiment, the grapevines were subjected to applications of 40 kg N ha^{-1} $year^{-1}$ (urea) and 20 kg K_2O ha^{-1} $year^{-1}$ (potassium chloride), according to the recommendation established by CQFS-RS/SC (2004). Phosphorus was never applied to the soil of the vineyards in the evaluated growth season.

2.3. Collection of grapevines and fractionation in organ

The grapevines were uprooted and partitioned at four phenological stages: flowering (F) (October 12, 2014), when 50% of flowers were open; veraison (V) (December 20, 2014), when 50% of berries changed color; harvest (H) (January 27, 2015) at which point 100% of the grapes showed intense color development; and dormancy (D) (April 11, 2015) (Baillod and Baggiolini, 1993). The grapevines were cut close to the soil surface, separated into roots, trunks, arms, spurs, new year shoots, leaves and clusters (when present in some phenological stages). The roots were collected in a 1.5 m^3 trench with a 0.7 m radius (the trunks was the central point) and 1.0 m depth. The roots were collected manually and stored. The trunks was cut close to the soil surface. The shoots were separated into new year shoots, spurs and arms. The leaves and clusters were cut at the intersection of the shoots and collected. All the organs were weighed in the field with the use of a hook digital precision scale. A subsample of each organ was collected, weighed and stored. The subsamples of the organs were dried in an oven with forced air at 65 °C until constant weight. Then the subsamples of dried organs were ground in a Wiley mill and passed through a 2 mm mesh sieve. Dry matter of different vine organs are presented in **Supplementary material 3.** Grape yield was 5.4 (±1.3) and 9.8 (±0.9) Mg ha^{-1} in V1 and V2, respectively (data not shown).

The tissue of the grapevine organs previously stored was subjected to chemical fractionation of P according to the methodology proposed by Casali et al. (2011). P forms obtained were: Total soluble P in acid (P_{ST}), inorganic soluble P in acid (P_{SI}), organic soluble P in acid (P_{SO}) (by the difference between P_{ST} and P_{SI}), lipid P (P_{LIP}), P associated with RNA (P_{RNA}), P associated with DNA (P_{DNA}) and residual P (P_{RES}). The determination and quantification of all P forms was done according to Murphy and Riley, 1962 in a UV–vis spectrophotometer.

2.4. Statistical analyses

The content of P forms (P_{ST}, P_{SI}, P_{LIP}, P_{RNA}, P_{DNA}, P_{RES}) in grapevine organs were subjected to analysis of variance using SISVAR (Ferreira, 1998). When the effects were significant by analysis of variance, the results obtained were subjected to a mean comparison test, based on levels of significance lower than 5% ($p < 0.05$) by Scott-Knott test (1974).

To compare the effect of the P content available in both vineyards, we made orthogonal contrasts by comparing the values of the P content of each fraction (P_{ST}, P_{SI}, P_{LIP}, P_{RNA}, P_{DNA}, P_{RES}) within each phenological stage, between grapevines grown in soil with low ($n = 3$) and high ($n = 3$) levels of available P.

To evaluate the distribution of P in vines during the production cycle, we used only P_{SI} and P_{SO} contents, as they contribute most to total P content and presented greater variation throughout the production period. We used Eq. (1) to calculate the percentages:

$$F\,(\%) = \frac{PFraction}{TotalP} \quad (1)$$

where: *F (%)* is the percentage of P in each fraction; *P fraction* is the P content of the fraction in mg kg^{-1} and total P is the P content in each organ in mg kg^{-1}.