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Effect of Soil Type on Calcium Absorption and Partitioning in Young Avocado (*Persea americana* Mill.) Trees

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Abstract: A two-year study was conducted to determine how soil texture affects calcium (Ca) absorption and partitioning in potted 'Hass' avocado trees. Trees were planted in 200 L pots in one of four soil types: clay (C), clay loam (CL), sandy loam (SL) or sand (S). Prior to planting, Ca content in each soil was in the normal range of availability, although the Ca concentration was highest in C soil. After two years of tree development, dry weights of shoots and roots were significantly higher in the SL and S soils than in C soil. Trees in the C soil had higher wood dry weight than trees in SL or S soils. The Ca contents (absolute quantities, not concentrations) in the roots, shoots and whole tree were significantly lower in the C soil than in the SL or S soils. The K/Ca ratio of trees in the C soil (K/Ca = 1.5) was significantly higher than that in the other soil types. Stem water potential was significantly lower for trees in the C soil compared to the other soils. These results indicate that Ca absorption and partitioning in young avocado trees varies with soil texture, probably associated with soil effects on root growth and/or plant water status.

Keywords: soil texture; avocado biomass; nutrient allocation

1. Introduction

In Chile, avocado production is located primarily in the Central Zone, a region where soil physical characteristics vary considerably [1]. Although most avocado orchards in this region are established in clay loam or clay soils, others are planted in sandy loam or sandy soils [2]. Avocado production in Chile has expanded to slopes of hillsides to avoid frost damage, but soils on these slopes can be limiting for avocado development due to their fine textures [3] that can restrict root growth and thus, nutrient absorption and biomass production.

Although avocado yield is highly dependent on climatic conditions and management, production potential is also related to soil characteristics such as soil macro-porosity (or air capacity) [4], pH, and availability of essential nutrient elements [5]. In Chile, growers often apply calcium (Ca), either as foliar sprays or soil applications [6]. However, in the avocado growing region of Chile, Ca in water and soil is abundant [7] and extra application of Ca seems not to be necessary. In fact, the avocado production area is concentrated mostly in alluvial formed soils from the Aconcagua and Maipo basins, with 80% of exchangeable Ca from total soil cation exchange capacity (CEC) [7]. However, Ca absorption not only depends on Ca availability in the soil but also, on several factors such as root growth flushes, transpiration and competition with other cations.

Avocado trees planted in fine-textured soils are prone to root hypoxia, which can negatively affect plant water relations by reducing the root water absorption capacity as a result of root damage and

reduced stomatal conductance (gs) and transpiration (Tr) [8–11]. Also, low soil air content (<17%) and/or low oxygen diffusion rates in the soil that are below 0.2 mg cm^{-1} min^{-1}, restrict avocado root growth [12], thus limiting plant water and nutrient uptake. Tzatzani et al. [13] recently found that nutrient uptake by avocado roots and/or translocation to shoots (stem and leaves) is dramatically reduced under conditions of high soil water content. Additionally, in fine-textured soils, root growth and metabolism are negatively impacted by resistance or impedance in the soil [14]. Plants respond to high impedance by ceasing root elongation, although root diameter is often increased when soil impedance is high.

Calcium is an essential nutrient, which is very important for tissue organization and physiological signal modulation as a secondary messenger [15]. Calcium is absorbed from the soil solution and delivered to the shoot in the xylem via the transpiration stream [16]. It may traverse the roots either through the cytoplasm of cells linked by plasmodesmata (the symplast) or through the spaces between cells (the apoplast) [16]. Calcium is an immobile nutrient; thus, once deposited in an organ, there is little to no redistribution [17]. Also, any factor that reduces transpiration, such as a decrease in the vapor pressure deficit between the leaf surface and atmosphere, or stomatal closure, can inhibit Ca transport from the roots to the leaves and fruit [18].

Calcium uptake by avocado trees can be limited by competition or antagonism with other nutrient elements. During nutrient uptake, an excess of Ca, magnesium (Mg) or potassium (K) may induce deficiencies due to antagonism between these elements [19]. Therefore, Ca, Mg, and K absorption from the soil depends not only on the concentrations of these elements in the soil, but on their ratios [20]. Calcium and Mg are passively absorbed by roots and compete for uptake with ammonium (NH_4^+) and K [21]. It has been reported in other species, such a plum (*Prunus domestica*) trees, that excessive K applied to the soil can interfere with Ca uptake and affect the Ca/K ratio in the fruit. Also, high nitrogen (N) concentrations in the soil can cause a dilution of Ca in the fruit flesh due to increased vegetative growth [22].

We hypothesize that the Ca content in avocado trees is not only related to Ca supply by the soil, but is dependent on root growth and absorption capacity, which in avocado, it is related to the soil air capacity and resistance to tree growth. The purpose of this study was to equate avocado Ca uptake and growth with soil type for soils typically found in the major avocado production region of Chile.

2. Materials and Methods

This two-year study was located in the Aconcagua Valley in the Central Zone of Chile (32°82′25″S 71°22′97″W), one of the main avocado productions areas of Chile. Four different soil types with different textures were collected from different avocado orchards in this area and steam sterilized to reduce the potential for soil-borne diseases. Several soil chemical characteristics were measured: pH (soil:water,1:2.5) (pHmeter Thermo Orion 3 Star), Organic Matter (OM) (Walky–Black wet oxidation method); N concentration was determined with a LECO CNS-2000 Macro Elemental Analyzer (Leco Corporation, St. Joseph, MI, USA); P (Olsen method). All exchangeable cations were also measured by extracting them from the soil with 1 N ammonium acetate at pH 7.0; extractions were then analyzed by ICP-Optical Emission Spectroscopy (model Agilent 720 ES axial spectrometer, Varian Inc., Victoria, Australia).

The soils evaluated were: clay (C), clay loam (CL), sandy loam (SL), and sandy (S) (Table 1). In September of Year 1 (spring in the Southern Hemisphere), one-year-old 'Hass' avocado trees grafted onto 'Mexicola' seedling rootstock were planted in pots made of white plastic mesh, supported by a wire structure, containing 200 L of soil.

The experiment was arranged in a completely randomized design, with one tree in each pot as the experimental unit (replicate) and 5 replicates per soil type. Prior to planting the trees, soil Ca content was determined to be in the normal range of availability in each soil according to Silva and Rodríguez [23]. However, C and CL soils had much higher initial Ca content than SL and S soils

(Table 1). Other chemical characteristics of each soil, including pH, organic matter (OM), N, P, K and Mg contents were also determined (Table 1).

Table 1. Physical and chemical characteristics of four soil types, derived from different orchards located in the avocado production region of Chile's Central Zone. Values represent means obtained from in situ and laboratory measurements. C (clay), CL (clay loam), SL (sandy loam), and S (sand), BD = bulk density, P = porosity, MP = macroporosity, OM = organic matter.

Treatment	Clay	BD	P	MP	pH	OM	N	P	K	Ca	Mg
	%	g cm^{-3}	%	%		%			mg kg^{-1}		
C	39.5	1.43	46.0	17.4	6.1	1.1	78	61	291	2020	172
CL	34.1	1.14	57.0	33.2	7.1	4.2	84	64	394	2160	194
SL	10.1	1.45	45.3	34.8	6.1	0.6	39	39	171	1320	145
S	7.5	1.38	47.9	31.4	6.6	0.3	55	30	183	1020	122

During the experiment, trees were irrigated with well water from the Aconcagua Basin with a drip irrigation system. Soil water content was monitored with frequency domain reflectometry (FDR) probes (Diviner, 2000; Sentek Sensor Technologies, Stepney, Australia). The irrigation frequency was varied among treatments in order to maintain all soil types near field capacity (−0.33 KPa). However, the total volume of water applied to each treatment was the same. During the first season, approximately 700 L/plant were applied; for the second season, irrigation water was approximately 1200 L/plant. The amount of leaching was not quantified.

During the experiment, trees were fertilized manually according to standard nutrient management practices for avocado orchards during the first years of development (without fruit production) [24]. Prior to fertilization, soil nutrient elements, except N, were at sufficient levels and did not limit tree growth [24]. During the first season, 4.2 g N/plant/week was applied and 6.3 g N/plant/week was applied during the second season. No Ca, except for the Ca contained in the irrigation water was applied to the plants. The amount of Ca applied in the irrigation water was calculated to be approximately 125 g/season/plant, based on 1257 L of water/plant/season and a Ca concentration of 100–120 mg Ca L^{-1} in the irrigation water.

One year after treatments were established, from November to March of the second season (spring and summer, Southern Hemisphere), plant water status was determined by measuring midday stem water potential (SWP) and stomatal conductance (g_s). Midday SWP was measured every fifteen days on three leaves per tree on sun-exposed branches on the external part of the canopy. Stem water potential was measured with a pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA, USA) using the protocol described by Ferreyra et al. [2]. Midday g_s was measured on mature leaves of ten randomly selected stems on the sun-exposed side of the tree with a steady state porometer (model Li-1600, Li-Cor Inc., Lincoln, NE, USA) as described by Prive and Janes [25] and Raviv et al. [26]. The g_s for each tree was the average of 3 leaves (one measurement per leaf). Net CO_2 assimilation (Pn) was measured once each month during the second season with an open system portable gas analyzer (model Li 6400, Li-COR Inc., Lincoln, NE, USA). Measurements were made from 10:00 to 13:00 hr on 3 mature leaves per tree, of similar size, with similar light exposure located in the middle of a spring shoot. Measurements were made at a photosynthetic photon flux (PPF) ranging from 1300 to 1900 µmol m^{-2} s^{-1}, a reference CO_2 concentration in the leaf cuvette between 375 to 400 ppm, and an air flow rate into the cuvette of 200 mmol s^{-1}.

At the end of the experiment (winter of year 2, Southern Hemisphere), trees were harvested and aerial parts were separated from the roots. Fresh weights of shoots and wood were determined with a digital balance. A "shoot" refers to the current season's branches plus attached leaves, and "wood" refers to the older trunk and branches. Roots were rinsed with tap water at a high pressure to remove soil particles. All organ samples were oven-dried at 70 °C for 3 to 4 days (to a constant weight) and dry

weights were determined with an electronic balance (Transcell ESW-5M, Transcell Technology, Inc. Buffalo Grove, IL, USA).

Calcium, Mg and K concentrations in each organ were determined after ashing tissues at 500 °C in a furnace (model 100, Naber, Valencia, Spain). Concentrations of these elements were then determined with an atomic absorption spectrophotometer (EAA Analyst 200, Perkin Elmer, Wellesley, MA, USA) according to the methodology described by the Analytical Association of Official Analytical Chemist (AOAC) [27]. For nutrient content (absolute quantity) determination, concentrations in each organ (%DW) were multiplied by the organ dry weight [28].

Data Analyses

Data were analyzed by one-way analysis of variance (ANOVA) and means were separated with a Tukey's honestly significant difference (HSD) test ($p \leq 0.05$) using Statistica 6.0 software (Statsoft, Tulsa, OK, USA). A Principal Component Analysis (PCA) was done, using Infostat 2018 (Infostat, FCA, Córdoba, Argentina), to identify associations between soil type and the dependent variables related to plant water relations, nutrition, and growth.

3. Results

3.1. Plant Dry Weight and Nutrient Content

Irrigation water and soil analyses indicated no chemical limitations to plant growth [23]. Total plant dry weight at the end of the experiment did not significantly differ among soil types. However, shoot and root dry weights were significantly higher in the SL and S soils compared to the C soil. Trees in the C soil had significantly greater wood dry weight than trees in the SL or S soils (Figure 1). Dry matter partitioning within trees was similar among CL, SL and S soils. However, trees in the C soil had more dry matter partitioned to the wood than the roots or shoots (Figure 2).

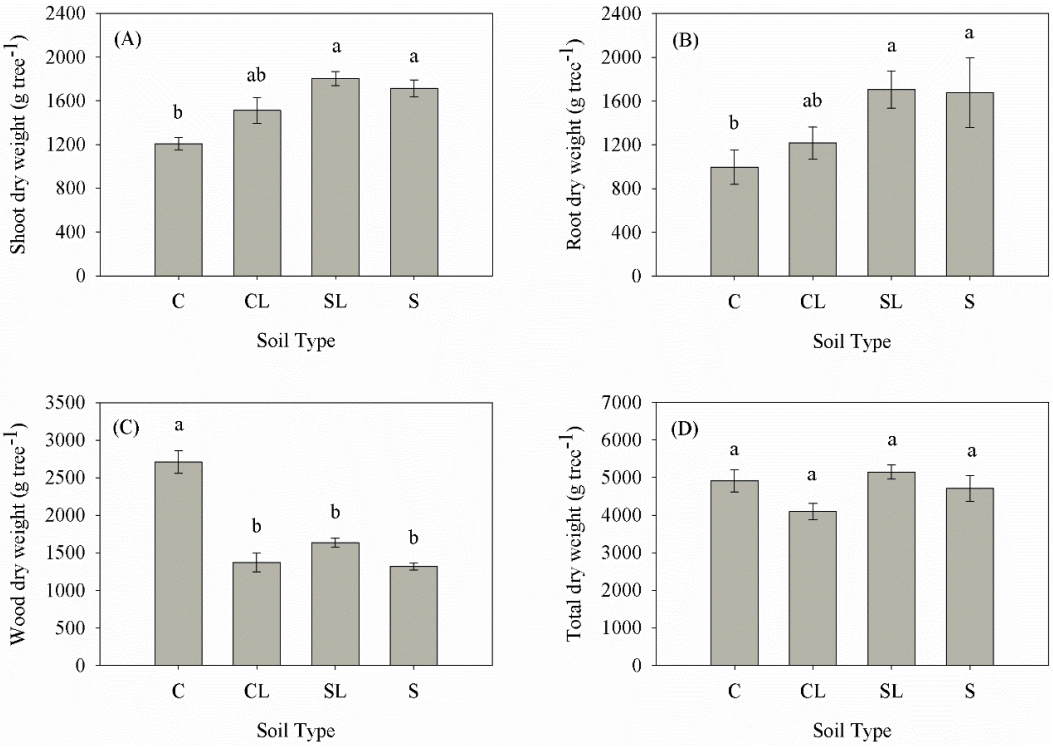

Figure 1. Dry weights (g tree^{-1}) of avocado plant tissues in four different soil types: C (clay), CL (clay loam), SL (sandy loam) and S (sand). (**A**) shoots, (**B**) roots; (**C**) wood; (**D**) total tree. Different letters indicate significant differences among soil types according to a Tukey's Honestly Significant Difference (HSD) test ($p \leq 0.05$). Bars represent means ± SE; n = 5.

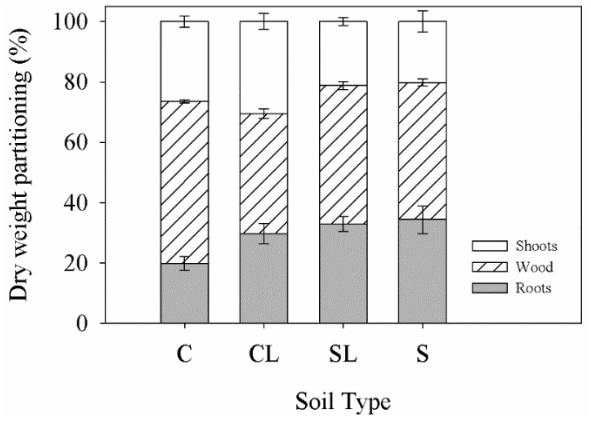

Figure 2. Dry weight partitioning among organs in avocado trees in different soil types: C (clay), CL (clay loam), SL (sandy loam) and S (sand); n = 5.

The Ca content (absolute quantity, g) in the roots, shoots, and whole tree were significantly lower in the C soil than in the SL or S soils (Figure 3). The K content in the shoots of plants grown in C soil were significantly lower than that of plants in CL, SL or S soils (Table 2). The K/Ca ratio in the CL, SL and S soils ranged from 0.8 to 0.9, with no significant differences in K/Ca among those three soil types. However, the K/Ca ratio was significantly higher in trees in the C soil than in the other soil types (Figure 4).

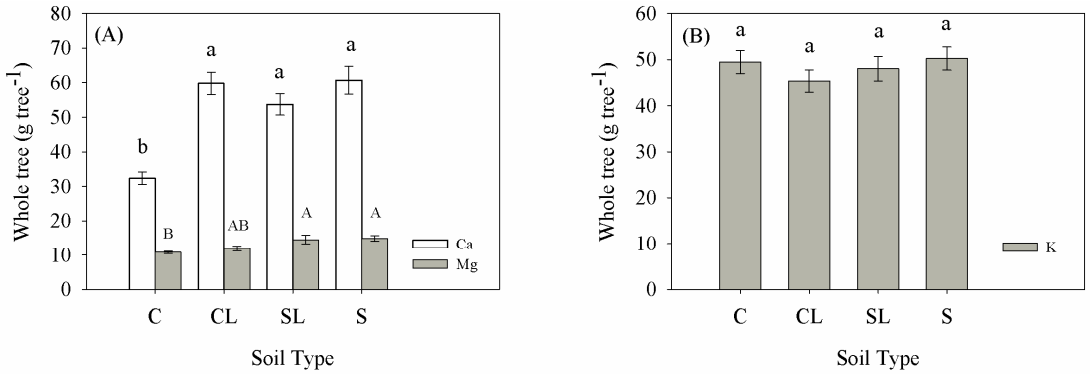

Figure 3. Calcium (Ca) and magnesium (Mg) contents (**A**), and potassium content (**B**) (g tree^{-1}) in whole avocado trees in different soil types: C (clay), CL (clay loam), SL (sandy loam) and S (sand). Different letters indicate significant differences among soil types (bars) for the same element according to a Tukey's Honestly Significant Difference (HSD) test ($p \leq 0.05$). Bars represent means ± SE; n = 5.

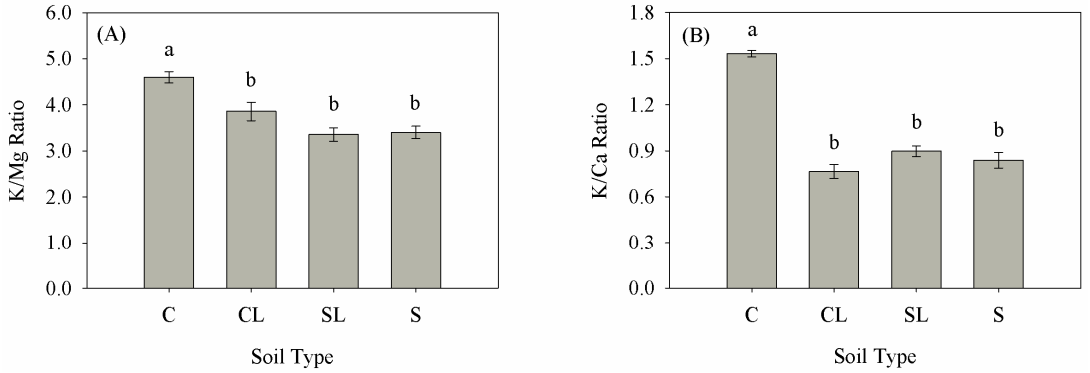

Figure 4. Potassium: magnesium (K/Mg) ratio (**A**) and potassium: calcium (K/Ca) ratio (**B**) in whole avocado trees in different soil types: C (clay), CL (clay loam), SL (sandy loam) and S (sand); n = 5. Different letters indicate significant differences among soil types according to a Tukey's Honestly Significant Difference (HSD) test ($p \leq 0.05$). Bars represent means ± SE; n = 5.

Table 2. Effect of soil type on nutrient content in different tissues of avocado trees. Values represent means ± standard error (n = 5). Different letters within columns indicate significant difference among treatments according to a Tukey's Honestly Significant Different (HSD) test, ($p \leq 0.05$).

		Nutrient Content (g)											
Element	**Treatment**	**Shoot**				**Wood**				**Root**			
K	C	14.5	±	1.0	b	29.3	±	2.5	a	5.7	±	0.9	ab
	CL	24.2	±	1.6	a	15.7	±	0.8	b	5.5	±	0.9	b
	SL	23.6	±	0.9	a	13.5	±	1.0	b	10.9	±	1.8	ab
	S	24.3	±	1.2	a	14.0	±	0.6	b	11.9	±	2.2	a
Ca	C	13.5	±	0.6	b	10.5	±	1.0	a	8.3	±	1.2	b
	CL	23.2	±	2.3	a	10.5	±	0.5	a	26.1	±	3.6	a
	SL	22.1	±	0.9	a	10.0	±	1.3	a	21.7	±	3.1	a
	S	25.6	±	0.9	a	9.9	±	0.6	a	25.1	±	3.9	a
Mg	C	4.1	±	0.2	c	4.1	±	0.2	a	2.5	±	0.3	b
	CL	4.6	±	0.4	bc	2.4	±	0.2	b	4.8	±	0.6	ab
	SL	5.8	±	0.2	ab	2.7	±	0.2	b	6.0	±	1.2	a
	S	6.2	±	0.4	a	2.7	±	0.1	b	6.0	±	0.9	a

3.2. Plant Water Status and Net CO_2 Assimilation

Soil texture affected plant water status and physiology, although results varied among the measurement dates (data not shown). In general, the SWP, gs, Tr and Pn were lower for trees in the C soil than in the other soils. However, significant differences were observed for SWP, gs and Tr only on the last measurement date in March of the second season (end of summer, Southern Hemisphere).

3.3. Principal Components Analysis

The PCA showed that Components 1 and 2 together explained 42% of the total variance of the data, with 24.8% explanation given to component 1 and 17.1% given to component 2 (Figure 5). The most heavily weighted observations correspond to S5 and C2, which correspond to sandy soil and clay soil, respectively. The PCA indicated that the variables positively associated with C soils were the K/Ca and K/Mg ratios, and volumetric and gravimetric water contents at field capacity (Vol MoistFC and GravMoist FC, respectively) (Figure 5). Soil macroporosity, shoot biomass, total biomass, Ca in shoots, wood biomass and total Ca content in the plant (Total Ca) were negatively associated with C soils but positively associated with S and SL soils (Figure 5). Thus, avocado trees in S and SL soils had greater growth and Ca absorption than trees in the other soil types, with Ca primarily allocated to the shoots (stem and leaves together) (Figure 5).

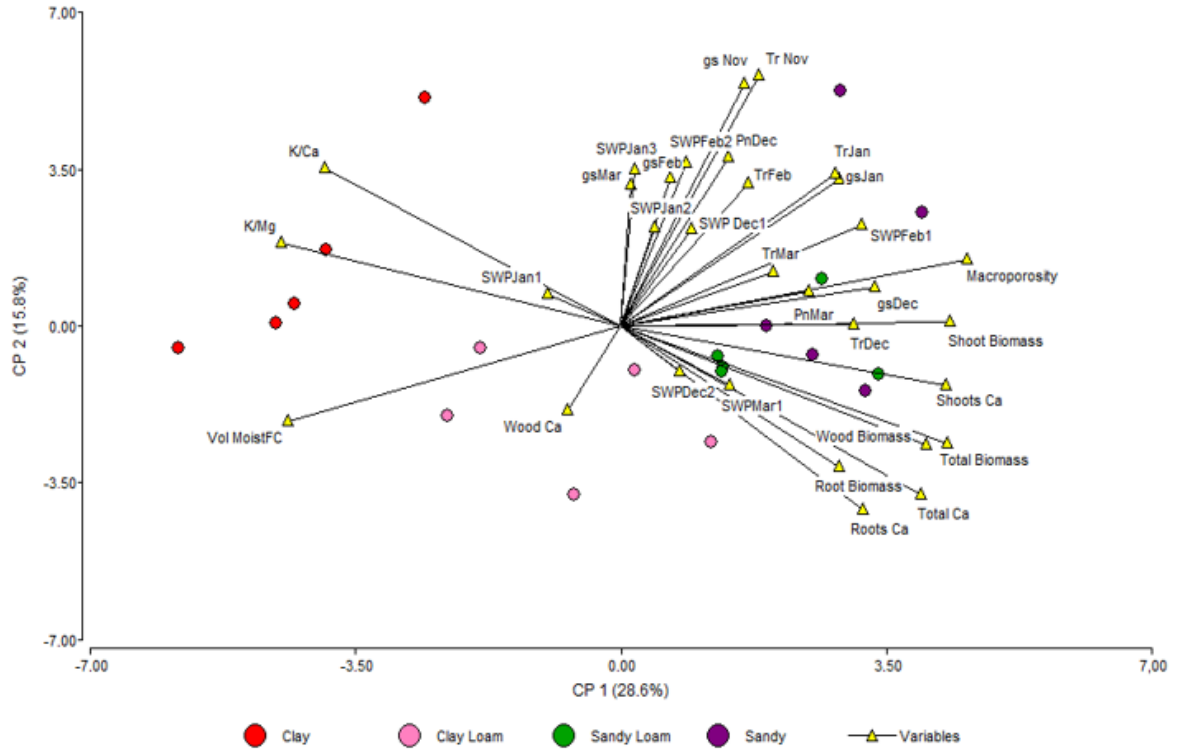

Figure 5. Principal Component Analysis of clay (C), clay loam (CL), sandy loam (SL), and sandy (S) soils. The variables that were grouped by soil type were: volumetric soil moisture at field capacity (Vol MoistFC), macroporosity, total Ca content in the plant (Total Ca), Ca content in the wood (Wood Ca); Ca content in the shoots (Shoot Ca); Ca content in the roots (Root Ca); plant K/Ca ratio, plant K/Mg ratio, total plant biomass, wood biomass, shoot biomass, root biomass, transpiration (Tr, from November to March); stomatal conductance (gs, from November to March), stem water potential (SWP, from December to March), net CO_2 assimilation (Pn, from December and March). Circles correspond to soil observations (red for C, pink for CL, green for SL and violet for S) and yellow triangles represent the measured variables.

4. Discussion

Although the clay soil had the highest Ca content, Ca uptake by avocado was lower in the clay soil compared with trees that were grown in the other soil types. The lower absorption of Ca in trees in the clay soil may have been due more to physical factors than to Ca availability or antagonism among nutrient elements in the soil. The lower macroporosity of clay soil could have caused a greater impedance for root growth [12,29], together with lower aeration of the rhizosphere [4], which could have affected both the vegetative and root dry weights, together with Ca absorption, even though this soil had higher concentrations of this element than the other soils.

Biomass increase and partitioning in avocado trees has previously been related to soil texture and the water to air ratio (W/A) in the soil [4]. The W/A is an indication of aeration capacity of a soil when it is kept at field capacity. It has been reported that clay and clay loam soils have relatively high W/A, which was associated with lower total avocado tree biomass, leaf area, and leaf retention compared to trees in sandy or sandy loam soils. This was related to a lower soil oxygen diffusion rate in clays soils than in the other soil types [4]. Srivastava and Singh [30] associated low yields in citrus species with poorly aerated fine soil textures and compacted soils, indicating poor root development, which affected water and nutrient absorption. Among nutrient elements for which uptake can be limited by soil texture, Ca and K have been indicated [31,32]. Other studies have shown similar results in other species. For example, Zhao et al. [33] reported that peanut growth and development differed among sandy, loam, and clay soils. In that study, even though soil OM, N, P and K contents were highest in clay and lowest in sandy soils, peanut growth and development were lower in clay soil, indicating that

the effects of soil texture on peanut growth and development is affected by the interaction between soil physical and chemical properties.

The texture of the clay soil may have affected Ca absorption not only because of its influence on root development associated with poor soil aeration but also, because of a greater impedance for root growth. Root growth and metabolism are greatly altered by soil impedance, and that condition is mainly influenced by the air space in the soil [12]. High root impedance may cause a cessation of root growth and/or changes in root metabolism and anatomy, such as swelling of cortical cells, increased ethylene production, accumulation of osmotic solutes in root apices, and a reduction in root length [34]. Reduced root growth not only affects water uptake but also, Ca absorption since Ca is absorbed at the new root apex zone, when the Casparian strip is not yet developed [34]. In avocado, a reduction of root growth can have dramatic effects on Ca uptake and plant growth, because unlike other woody species, avocado lacks root hairs [35] and thus, water and nutrient absorption may be low compared to other species subjected to the same conditions.

There are two pathways for the radial transport of ions from the epidermis to the endodermis through the cortex of plant roots. Apoplastic transport is through the free space of the root cortex, specifically through the continuum of cell walls and lacks intercellular flux resistance until the flux reaches the endodermis where the Casparian strip is located [34]. Symplastic transport occurs through the cytoplasm of the cells [36]. There is little information about the exact zone for Ca absorption in avocado trees. In other woody species such as grapevine, it has been reported that Ca uptake at the root tip is high and Ca accumulated mainly in root cells of the terminal 5 mm (inclusive of the root cap) [37]. Other authors have stated that the typical profile of Ca uptake along the roots is over the first 2 mm [38]. Radial transport of Ca in avocado trees is through the apoplast. Thus, mature endodermal tissue in the roots becomes inaccessible to Ca. Calcium transport to the stele region is possible only in some immature portions of the endodermis, which is scarce in mature roots [39]. In avocado trees, Ca uptake could have been lower in clay soils partly because reduced root growth in this soil type limited the effective absorption area of the roots.

The apoplastic pathway is not only important for Ca uptake but also, for water absorption [40]. Calcium supply in plants is often tightly linked to transpiration [41,42]. Therefore, a low Ca content in avocado trees in clay soils could be due also to a reduction in water uptake by the plant.

The K/Ca and K/Mg ratios were significantly higher avocado trees in clay soil compared to the other soil types (Figure 4). Trees in clay soil had a 1.5 times higher K/Ca ratio despite the higher Ca and lower K concentrations in the clay soil compared to the sandy loam and sandy soils. It is well known that K, Mg and Ca share the same binding sites to soil particles, and, therefore, an excess of some of these elements can affect the availability of the other cations in the soil [43]. This antagonism is strong in the case of K versus Mg, but it has also been observed between K and Ca [44]. In the present study, trees growing in soils with higher Ca and Mg concentrations had higher K/Ca and K/Mg ratios, which could not be attributed to competition among binding sites in the soil. The differences in plant K/Ca ratios could be more attributable to the root absorption capacity and Ca transport within the plant. Absorption of Ca is more affected than the absorption of K, possibly because Ca absorption is very dependent on the growth of new roots and Ca mobility is mainly through the xylem and depends on transpiration, whereas K is actively absorbed through the plasma membrane of the epidermis cells in the root [35]. Potassium also is preferentially distributed within the cells especially, in the inner area of the root than at the cell wall, and thus is not necessarily dependent on the xylem sap flow rate [35].

Biomass partitioning is an important factor to be considered in Ca uptake and distribution. In the present study, avocado trees planted in clay soil (C) had more biomass partitioned to the woody portion of the trees, and less partitioned to the "annual" organs such as shoots and roots. Bonomelli and Artacho [45] reported that in young cherry trees (age 1–3 years) fine and main roots represented approximately 30% of the biomass of trees in unrestricted soils, similar to the observed proportion found in this study for avocado trees in CL, SL and S soils. In the clay soil, avocado roots reached only

20% of the total biomass, probably due to the mechanical impedance and/or lack of aeration caused by low soil macroporosity [34].

The results of this study indicated that Ca absorption and biomass partitioning in avocado trees varies with soil texture. Calcium absorption is lower in soils with higher clay content, which was associated with a lower macroporosity compared to the other soil types evaluated. In sandy and sandy loam soil, the Ca was allocated principally to shoots and roots, but in clay soils, Ca was mostly allocated to the wood. According to the PCA, soils in the Chilean avocado production areas with sandy and sandy loam soils were associated with greater plant biomass, Ca absorption, and macroporosity than areas with the other soil types tested, whereas clay soils were associated with low root, shoot and whole-plant Ca contents and are positively associated with higher soil water content at field capacity. Some variables related to water status (gs, SWP) were significantly and positively associated with Ca in shoots in sandy and sandy loam soils but not in clay soil (Figure 5). This confirms previous observations that absorption of Ca in woody trees is related to xylem sap movement, which in the case of avocado, is highly dependent on the air capacity of the soil [1,4,8,9]. This general overview of the influence of soil type on tree nutrition, water status and growth variables suggests that Ca content and partitioning is highly dependent on soil macroporosity and its interaction with plant physiological and growth responses.

5. Conclusions

The total plant biomass of avocado was similar among trees grown in the different soil types tested in this study; however, biomass partitioning varied among soil types. The amount of biomass partitioned to the wood was significantly lower in sandy soils compared to clay soil. However, root and annual growth (shoots) were significantly lower in clay than in sandy soils. Root, shoot and total tree Ca content was significantly lower in the clay soil compared with the sandier soils. For trees in the CL, SL and S soils, the K/Ca ratio was close to 0.9, but in trees in the clay (C) soil, the ratio was 1.5. Thus, absorption and partitioning of Ca in avocado trees was clearly affected by soil texture.

The results of this study indicate that Ca absorption and biomass partitioning varies with soil texture, probably associated with soil resistance to root growth and/or root oxygen conditions for water and Ca absorption. Therefore, Ca nutrition in avocado orchards planted in soils in the main Chilean avocado production region is not an issue of Ca supply in the soil, but is related to soil conditions for Ca absorption.

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