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Short Communication

EFFECTS OF SOWING DEPTH ON REMOBILIZATION AND TRANSLOCATION OF SEED PHOSPHORUS RESERVES

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ABSTRACT

Sowing depth can affect seedling establishment due to poor remobilization and translocation of seed reserves towards newly growing maize seedling sinks. A pot study was conducted to investigate the relationship between seedling phytomass and phosphorus (P) source-sink as affected by three sowing depths. Uniform maize seeds were planted in plastic pots at 2, 5 or 8 cm sowing depths and placed in a completely randomized design. Results revealed that seed phytomass, P hydrolysis and P translocation to newly growing sinks were significantly ($p \leq 0.05$) higher at shallow sowing depths compared to deeper ones. Seed P source was efficiently utilized by seedlings at 2 cm depth due to higher P loading to leaves (60%) and roots (34%). However, developed seedling sinks at deeper depths caused a significant increase in leaf P concentrations, expressing a poor utilization of P source in terms of seedling phytomass. Results suggested a good relationship of source-sink for P remobilization and translocation at shallow showing depth and sowing seeds at 2 cm depth could results in better source P utilization and healthy crop stand for sustainable agriculture.

Key words: Emergence, phosphorus, phytomass, remobilization, sink, source, sowing depth, Zea mays.

INTRODUCTION

Germination is the first step in the successful life cycle of green plants. It is a complex phenomenon in which the mature dry seeds pass from a state of quiescence, where the metabolism is virtually halted in a state of intense metabolic activities (Bewly, 1997). Besides the basic requirements for water, seed germination depends upon on both internal and external factors (Sikder *et al.,* 2009; Motsa *et al.,* 2015; Penfield and MacGregor, 2017). Being important macronutrients, endogenous seed carbon (C), nitrogen (N) and phosphorus (P) can greatly affect seed germination, emergence as well as seedling establishment. Phosphorus is one of the major components of all basic cell structures and developing seedlings depend mainly on stored seed P reserves located in scutellum during few weeks of early maize seedling growth (Nadeem *et al*., 2011). Seed C, N and P starts to remobilize soon after the seed imbibition and supports the developing seedling sinks (Nadeem *et al.,* 2011). Seed P remobilize rapidly and translocate towards emerging seedling sinks, and is the main source to sustain early plant growth. Thereafter, this P source is supplemented by autotrophic P uptake by developing seedling roots (Nadeem *et al*., 2014). Sowing depths can greatly influence the seedlings ability to emerge and establish a uniform relationship among seed nutrient source and seedling nutrient sinks (Behtari and Luis 2012; Zuo *et al.,* 2017). Therefore, seed sowing at uneven or deeper depths could result in complete failure of seedling emergence despite the seeds completing their germination (Seeiso and Materechera 2011; Guojun *et al.,* 2015). Hence, it is important to plant seeds at proper depth in order to achieve good emergence rate and healthy seedling stand. The sowing depth is also important in terms of utilization of seed P source during germination and its distribution among seedling leaves and roots. Since seed P remobilization may be affected with sowing depths, therefore (i) seed P reserves and phytomass remobilization, and (ii) their translocation towards developing seedling roots and leaves is of prime importance. Although literature is replete with information regarding effects of sowing depths on crop growth and final harvest, however, there is dearth of knowledge on the remobilization of seed P, their translocation towards seedling sinks and phytomass accumulation. Therefore, a study was planned to evaluate the effects of different sowing depths on source-sink relationship for P and phytomass in newly growing maize seedlings.

MATERIALS AND METHODS

The study was carried out in the greenhouse during August 2009, at INRA Bordeaux, France. Uniform seeds (cv. DKC-5783 Dekalb Monsanto Agricoltura SpA. Lodi Italy) with the homogenous seed weight (0.311 g ± 0.001) and size were sown in small (10×10×14 cm) opaque polypropylene pots containing fine sand and a complete nutrient solution (Bhadoria *et al*., 2004). The experiment was comprised of three sowing depths (2 cm, 5 cm, 8 cm) and each treatment was replicated in triplicate. There were a total of 45 maize seeds in 9 pots placed in a completely randomized position in the greenhouse. The pots were filled with fine sand (1660 g pot^{-1}) and five pre-imbibed seeds in distilled water (5 min) were sown at 2 cm, 5 cm and 8 cm sowing depths for each treatment. A measured volume of nutrient solution (300 mL pot^{-1}) was added to each pot to reach a 90% saturation capacity of sand. All pots were placed under light (High Pressure Sodium Lamp-400 W) and were irrigated each day based on water lost by evapotranspiration from each pot. The seedlings were grown for 16-days of early growth and seedling emergence was noted each day based on emerged seedlings from sand surface. On day 16, all seeds and seedlings were removed gently from sand and germination count was recorded in each treatment. Emergence percentage was also noted keeping in view the total number of germinated and emerged seeds excluding dormant ones. Thereafter, seedlings were washed with distilled water and separated into five seedling compartments including seed endosperm, seed scutellum, coleoptile, roots and leaves. Fresh phytomass (*biomass*) was measured and all seedling compartments were lyophilized for 24 h to record dry phytomass (g seedling^{-1}). Phosphorus concentrations in each seedling compartment were analyzed by malachite green colorimetric technique (Van Velhoven and Mannaerts 1987). Briefly, each seedling part was ground separately (Retsch MM400 mixer mill), and a weighed sample then reduced to ashes at 550 °C for 5 h. Phosphorus mineralization was carried out with HNO_3 and P contents were measured taking into account the phytomass of each seedling compartment. All the data were analyzed by ANOVA using R environment software. Means were compared using Tukey's test at the 0.05 probability level.

RESULTS AND DISCUSSION

Dynamics of seedling emergence and seed germination: Germination and emergence are two critical phases involved in the better seedling stand and higher crop yields (Bewley, 1997; Zhang, 2001; Jeremi, 2017). We have defined seed germination as rupture of seed coat and elongation of embryonic axis (coleoptile and radicle) based on the definition by Bewley (1997), whereas, seedling emergence is characterized when seedling coleoptile reached soil surface. Higher seed germination percentage was noticed at deeper sowing depths (73%) than at 2 cm deep sown seeds (67%) after 16 days of sowing (Figure 1a). Although the germination percentage was higher at 5 cm and 8 cm, however, seedling emergence was quite low at deeper sowing depths (Figure 1b). Wang *et al*. (2016) reported that seed germination and seedling emergence is adversely affected by sowing depths and deeper sown seeds caused a delay in seedling to reach soil surface. Maximum emergence (100%) was recorded on day 5th at 2 cm depth, however emergence was delayed up to day 8 (18%) at 8 cm and up to day 9 (82%) at 5 cm sowing depth (Figure 1b), and similar results were reported by John *et al.* (2013). Endogenous seed nutrient reserves are the main driving force for early seedling nutrition and help seedlings to reach soil surface (Modi and Asanzi 2008; Nadeem *et al.,* 2011; Zuo *et al.,* 2017). Although deep sown seeds attained higher germination percentage, however the seedlings have to exert an extra force to traverse from deeper soil surface by utilization more seed reserves as concluded by other researchers (Mahdi *et al.,* 1998; Tobe *et al.,* 2007; Zuo *et al.,* 2017). In addition, the seeds planted at deeper depths displayed the slow remobilization of the stored C reserves due to poor development of seedling sinks including roots and leaves (Figure 2b).

Dynamics of seed phytomass remobilization and seedling phytomass accumulation: Imbibition of dry seeds initiates the enzyme activation, hydrolysis of stored seed reserves and their translocation to plantule which further rupture seed covering to emerge from seed coat (Bewley, 1997). Maize seeds placed at 2 cm sowing depth expressed remobilization of stored C from very first day after sowing (Nadeem *et al.,* 2011). Such changes caused the emergence of seedling radicle and first leaf from seed coat on second and third day after sowing, respectively (Nadeem *et al.,* 2011). In current study, we have observed significantly higher seed phytomass loss than seedling phytomass accumulation at deeper depths than at shallow sowing depth of 2 cm (Figure 2a). It is also obvious from less developed seedling roots and leaves at deeper sowing depths compared to 2 cm planted seeds (Figure 2b). Earlier studies reported such C losses are due to seed respiration and allocation of seed C to developing sinks such as coleoptile, roots and leaves (Nadeem *et al*., 2014; Sime *et al.,* 2016). Seed C loss is significantly higher than seedling C accumulation from 4th to 14th day after seeding when seeds placed at 2 cm sowing depths (Nadeem *et al.,* 2014). Higher seed phytomass loss than seedling phytomass accumulation at deeper sowing depths depicted more phytomass utilization by seedlings to overcome seeding depth stress (Figure 2a). After 16 days of early growth, only 10%, 14% and 16% of initial seed phytomass reserves (0.311 ± 0.001 g seed^{-1}) were noticed in seed endosperm and scutellum at 2 cm, 5 cm, and 8 cm respectively (Figure 2b). Higher reserves remaining in seeds at deeper depths expressed poor utilization of all reserves in terms of seedling phytomass accumulation than shallow depth (Figure 2b). The remobilized reserves were allocated to seedling sinks including roots and leaves as depicted in Figure 2b. However, significantly ($p \leq 0.05$) higher phytomass was translocated towards seedling roots and leaves when seeds were placed at 2 cm depth compared to 5 cm or 8 cm (Figure 2b). Seedling translocated phytomass equally among roots and leaves when planted at 2 cm sowing depth, whereas the phytomass translocation was slightly higher among leaves than roots at 5 cm and 8 cm (Figure 2b). Such preferences of seedlings to translocate more phytomass reserves to leaves than roots at deeper sowing depth express their tendency to reach soil surface for photosynthesis as also depicted from higher seed phytomass loss (Figure 2a). John *et al.* (2013) reported similar results that increasing seeding depth from 10 mm to 100 mm caused an increase in partitioning of phytomass to seedling leaves from 23.6% to 26.1% at the cost of root phytomass decrease from 69.5% to 57.9%. Shallow sowing seeds resulted in healthy seedlings in terms of seedling length, number of leaves, leaf area and phytomass compared to deeper sown seeds (Sime *et al.,* 2016). The equal translocation of seedling phytomass to leaves and roots at shallow depth (2 cm) indicated seedling's better utilization of phytomass reserves and photosynthesis abilities under non-stressed growth conditions compared to deep sowing depth. However, seedling coleoptile was a smaller seedling phytomass sink and varied from 6% to 17% of seedling phytomass at different sowing depths (Figure 2b).

Dynamics of seed P remobilization and seedling P accumulation: Endogenous seed P reserves are the principal contributors for seedling P demands during first few weeks during early maize seedling growth (Nadeem *et al.,* 2011). Phosphorus isotopic techniques indicated a significant autotrophic P uptake by seedling roots from 5th day after sowing when seeds were placed at 2 cm depth (Nadeem *et al.,* 2014). Significantly, lower P accumulation was recorded in seedlings grown at deeper sowing depths than at 2 cm (Figure 3a). Such P losses were 19%, 17%, and 8% of total initial seed P stock (730.11± 24 µg seed^{-1}) at 8 cm, 5 cm and 2 cm sowing depths, respectively (Figure 3a). Seed P loss was assumed to be due to P translocated to developing seedling compartments plus possible P efflux which was reported up to 40% of initial seed P stock (Nadeem *et al.*, 2012). Significantly, lower P was noticed in seed P sources (scutellum and endosperm) after 16 days of early growth when seeds were sown at 2 cm compared to 5 cm or 8 cm (Figure 3b). Such decrease in seed P sources corresponds to allocation of P towards developing seedling sinks including roots and leaves (Figure 3b). Significantly, higher P accumulation was noticed in developing seedlings at shallow sowing depth compared to 5 cm and 8 cm after 16 days of early growth (Figure 3b). Significantly higher seed P reserves remobilized and translocated towards newly developing seedling sinks. However, translocation to leaves was significantly higher than roots irrespective of sowing depths. Seedlings grew actively at shallow sowing depth and reached soil surface to participate actively in photosynthesis, where P is the key nutrient involved in leaf gas exchange process (Augé *et al.,* 2016). Vandamme *et al.,* (2016) also reported a strong correlation between seedling leaf P contents and phytomass during 6 weeks of early growth. However, seedlings utilized more P in growth to enable developing coleoptile enclosing first leaf to traverse from deeper soil layers justifying seedling preference to allocate higher P to leaves rather than roots at deeper sowing depths (Figure 3b). Once coleoptile reaches soil surface, seedlings preferably allocate more phytomass and P to leaves and leaving behind coleoptile as a minor P sink in terms of P allocation (Figure 3b). A majority of the total seedling P (60 – 62%) was translocated towards major P sink (leaves) and only 28 – 34% was translocated to roots, whereas seedling coleoptile received only a 4% to 14% share of total seedling P reserves (Figure 3b). We earlier reported that seedlings allocate more P to leaves than roots, being a major site of photosynthesis where P is required in macro quantities when seeded at 2 cm sowing depths (Nadeem *et al*., 2013). Significantly higher P concentrations were recorded in seedling (leaves: 1939±468 µg g^{-1}; roots: 912±178 µg g^{-1}; coleoptile: 1194±445 µg g^{-1}) when sown at 8 cm sowing depth compared to 5 cm (leaf: 1043±150 µg g^{-1}; roots: 613±172 µg g^{-1}; coleoptile: 892±128 µg g^{-1}) and 2 cm (leaf: 915±269 µg g^{-1}; roots: 468±195 µg g^{-1}; coleoptile: 530±194 µg g^{-1}). Such P concentration differences in roots and leaves at deeper sowing depths were verified from the seedling phytomass accumulation abilities, which is significantly lower at deeper sowing depths than at 2 cm (Figure 2b). In the case, when seeds are sown deeper the seedlings have to traverse the thicker soil layer causing low phytomass accumulation in seedlings (Tobe *et al.,* 2007; Jeremi, 2017), therefore, P dilution could not occur efficiently under low restricting phytomass accumulating conditions at deeper sowing depths (Figure 2b). At shallow sowing depth, seedlings developed their leaves and roots properly with higher phytomass also described by John *et al.,* (2013) and Sime *et al.,* (2016), and therefore utilized the remobilized seed P reserves efficiently, and have lower P concentrations. The seedling leaf P concentrations were higher than the lower P limits where seedlings start to halt their growth due to P deficiencies (White and Brown 2010).

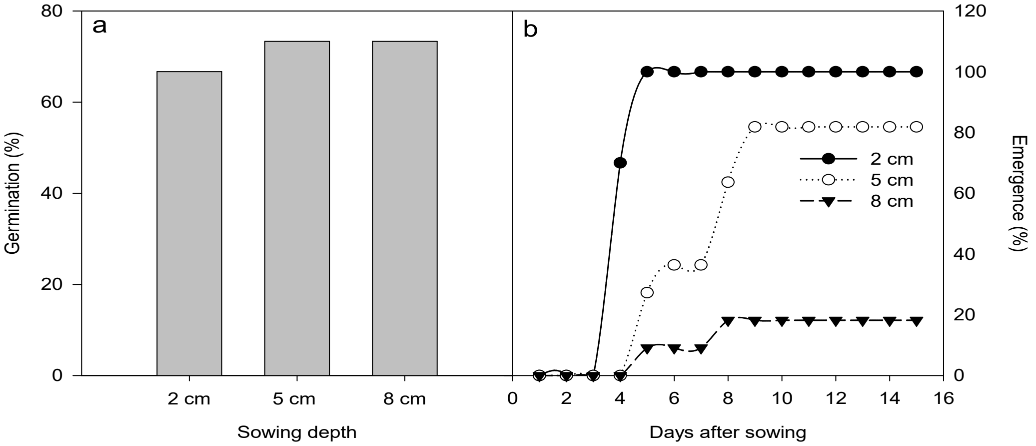

Figure 1. Effect of different sowing depths (2 cm, 5 cm, 8cm) on dynamics of seed germination (a), and seedling emergence (b) during 16-days of early maize seedling growth. Seedling emergence is defined as the emerged seedlings out of total germinated seeds.

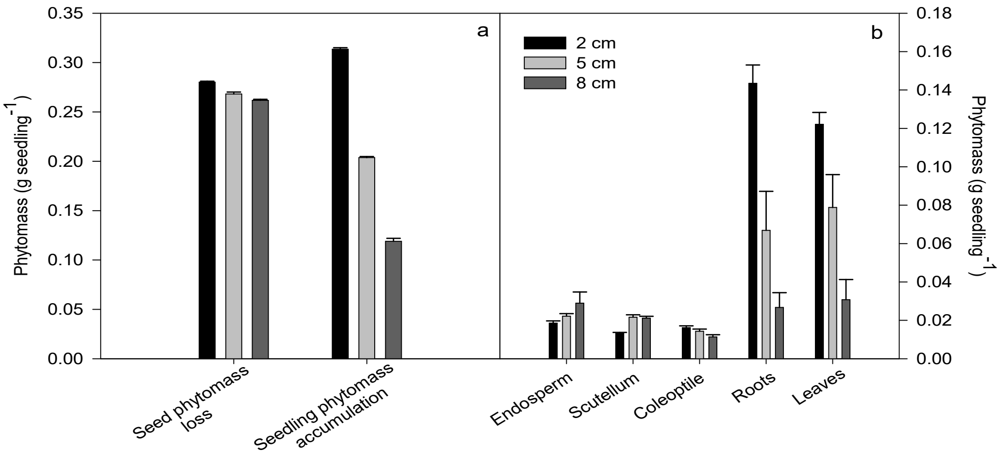

Figure 2. Effect of different sowing depths (2 cm, 5 cm, 8 cm) on the dynamics of seed phytomass loss and seedling phytomass accumulation (a), and seed phytomass allocation to different sinks in 16-day old maize seedling (b). Data are means and bar errors indicate standard error of three replications.

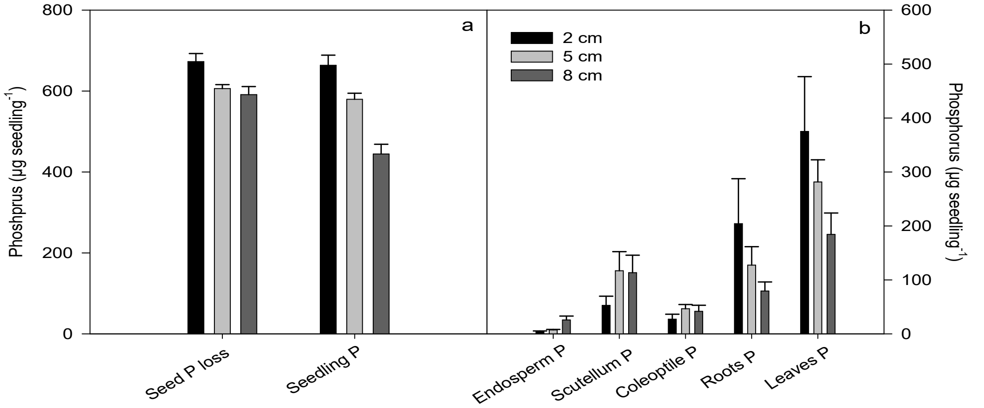

Figure 3. Effect of different sowing depths (2 cm, 5 cm, 8 cm) on the dynamics of seed phosphorus loss and seedling phosphorus accumulation (a), and seed phosphorus allocation to different sinks in 16-day old maize seedling (b). Data are means and bar errors indicate standard error of three replications.

Conclusion: Early seedling growth is most important for determining final crop harvest. The important objective of sustainable agriculture is to put seeds at proper sowing depth for germination, emergence and efficient linkage between seed nutrient source and seedling nutrient sinks. Remobilization and efficient use of seed P reserves is especially critical for seedling growth before P uptake by roots become effective. Sowing depth affects the seed P source utilization, so that the P issue should be considered when looking for an optimum sowing depth.

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