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EFFECTS OF PHOSPHORUS AND DROUGHT STRESSES ON DRY MATTER AND PHOSPHORUS ALLOCATION IN WHEAT

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ABSTRACT: The effect of phosphorus (P) and soil water availability (W) on the growth and development of wheat plants (*Triticum aestivum* L. cv. Minaret) was studied in a pot experiment. Four levels of P supply (0, 15, 30, and 100 µgP/g soil) were applied before sowing. Thirty-four days after sowing (DAS), the pots were kept near 100% of field capacity (FC). From 34 DAS until one week before anthesis (67 DAS), half of the pots were maintained between 60-70% FC. Control pots were kept at 85-95% FC by weighing and watering the pots every two to three days. Shoots were harvested four times before anthesis and twice after. At each harvest, dry matter and P accumulation were measured in leaves, stems, and ears. In this study, thermal time until anthesis was inversely related to the level of P application. Phosphorus additioning affected the allocation of biomass and P in aerial plant organs. Plants growing only with soil P showed a delay in the allocation of dry matter and P into leaves and stems with respect to plants fertilized with 100 µg P/g of soil. In this study, the final composition of the grain depended on re-mobilization from other plant organs. Evidence of independent re-mobilization of carbohydrates and P towards the ear is presented, and the pattern of plant development as well as the relationships between development and dry matter and P allocation are discussed.

INTRODUCTION

Although it has been stated, for wheat and barley, that temperature and photoperiod are dominant factors influencing the rate of plant development (1), it

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has also been observed that the nutritional and hydric status of the plant can affect its rate of phenological development (2,3). More recently, Squire (4) mentioned that under nutrient deficiency the period between sowing and flowering increases and that of grain filling changes little or decreases. During the plant's life cycle, developmental controls operate to alter the allocation of dry matter and nutrients among alternative sinks. Early in plant development, allocation towards vegetative organs is high, and after anthesis, ears become the main sink for nutrients and carbohydrates. The proportion of total dry matter and nutrients accumulated by harvested plant organs is largely determined by factors controlling carbon (C) partitioning between alternative sinks (5). Plants have adaptative mechanisms by which they can respond to stresses, thereby improving their chances of survival or yield, and many of these mechanisms involve changes in partitioning (6). It has been shown that under nitrogen (N) or P starvation (7), or water limitation (8), dry matter allocation to the roots is increased, allowing for a relatively more intense root exploration for soil resources (9). This kind of response was early given a functional interpretation (10), more recently more complex models based on carbon-nitrogen-water interactions have been proposed by Dewar (11). Nevertheless, it is surprising that the analysis of the relationships between P shortage, plant development, and dry matter and P allocation to different aerial plant organs have had little attention until now. In this study, we dtermined the relationships between plant development and allocation of dry matter and P into different aereal organs under contrasting levels of soil P and water availability.

Phosphorus is a relatively mobile element in plants, moving easily between organs. Ultimately the grain becomes the major sink for P, and at maturity, it may contain up to 90% of total shoot P (12). Phosphorus concentration in grains is important particularly in seed multiplication stands, and in situations where there is little nutrient uptake after ear emergence. Marshall and Wardlaw (13) observed that the movement of P from leaves during grain filling was largely determined by the movement and demand for carbohydrates within the plant, and not by a P requirement of the sink. However, the validity of such a statement would not apply under P-limiting conditions (14). The differential retention of P and C in the flag leaf of wheat plants was observed by Batten and Wardlow (14) in low P-containing plants, would evidence that retranslocation of C and P from the leaves to the grain is not completely interdependent. In this study, we also present evidence that strengthens the view of an independent re-mobilisation of P and dry matter towards the developing ear under different levels of P and water availability.

MATERIALS AND METHODS

Wheat plants (*Triticum aestivum* L. cv. Minaret) were grown in pots under a rain-shelter during the spring of 1993 in Wageningen, The Netherlands. Treatments consisted in the combination of two factors: P addition (four levels) and soil water availability (two levels). Pots, 28 cm height and 21 cm diameter, were filled with an homogeneous mixture of sand and a sandy soil (3:1). The sandy soil contained 50 μg P/g soil (Bray and Kurts I), while the P content of the sand was negligible. The levels of added P per soil mass were 0, 15, 30, and 100 μg P/g soil, (P0, P15, P30, and P100, respectively). The fertilizer was thoroughly mixed within the first 15 cm of each pot, using finely ground super phosphate. Soil water content at field capacity (FC) was determined by applying 300 mL of water to a pot of 1,000 g of the soil mixture, allowing drainage for 24 hrs, and weighing. Between sowing and 28 days after sowing (DAS), all pots were kept near 100% of field capacity. At 34 DAS, half of the pots were brought to 85-95% FC, and the other half to 60-70% of FC by weighing and watering the pots two to three times a week.

Before sowing and after each harvest, pots were supplied with 75 μg N/g soil (as ammonium nitrate) and 75 μg K_2O/g soil (as K_2SO_4). At sowing, the following solution with micronutrients was applied: B = 0.1 μg/g soil as H_3BO_3; Mn = 0.1 μg/g soil as $MnCl_2{\cdot}4H_2O$; Cu = 0.1 μg/g soil as $CuSO_4{\cdot}5H_2O$; Zn = 0.5 pμ/g soil as $ZnSO_4{\cdot}7H_2O$; Mo = 0.005 μg/g soil as $(NH_4)_6Mo_7O_{24}{\cdot}4H_2O$; and Fe = 6.1 μg/g soil as Fe-EDTA. Five pregerminated seeds were sown on March 19 which emerged after nine days. On April 7, the pots were thinned to three plants per pot.

The experiment had a completely randomized factorial block design with three replications per treatment. All the measurements are expressed on a per plant basis, each replication was the average of three plants per pot. There were six harvests of shoots at 34, 49, 57, 67, 90, and 115 DAS. One row of pots was set around the experiment as a boundary.

The effects of P and water supply on plant development were studied through their effects on the thermal time required to reach certain developmental stages (anthesis), and the appearance of leaf tips on the main stem. For the calculation of the cumulated thermal time, a constant base temperature of 0°C was used. Plant growth and dry matter allocation was studied by measuring the leaf area, and the dry weight of leaves, stems (including sheaths), chaff, and grains. Total P content in the different plant organs, except roots, was measured after wet digestion of dried sub-samples in a H_2SO_4-Se-salicylic acid mixture with addition of H_2O_2. Total P was determined by the colorimetric molybdenum-blue method.

Dry matter (DMA) and phosphorus (PA) allocation to different plant organs were calculated as:

$$\mathrm{DMA} = \frac{(\text{Dry weight organ})_{t2} - (\text{Dry weight organ})_{t1}}{(\text{Dry weight shoot})_{t2} - (\text{Dry weight shoot})_{t1}}$$

where **t1** and **t2** are consecutive harvests.

$$\mathrm{PA} = \frac{(\text{P content organ})_{t2} - (\text{P content organ})_{t1}}{(\text{P content shoot})_{t2} - (\text{P content shoot})_{t1}}$$

We also considered that all the lost dry weight from vegetative organs after anthesis was translocated to the grain, while Austin et al. (15) calculated a respiration lost of 17%. The proportion of dry matter remobilized (PRDW) allocated in the ears was calculated as follows:

$$\mathrm{PRDW} = (\mathrm{RDW})/(\mathrm{EDW}) \times 100$$

where: **EDW** is the dry weight of ears at final harvest (g/plant), and **RDW** is the dry matter re-mobilized from leaves (l) and stems (s) (g/plant). The amount of dry matter re-mobilized (**RDW**) from leaves or stems was calculated as:

$$\mathrm{RDW}_l = \mathrm{LDW}_{90} - \mathrm{LDW}_{115}$$

$$\mathrm{RDW}_s = \mathrm{SDW}_{90} - \mathrm{SDW}_{115}$$

where: $\mathbf{LDW}_{90}$ and $\mathbf{LDW}_{115}$ are the dry weight of leaves (g/plant) at 90 and 115 DAS, respectively; $\mathbf{SDW}_{90}$ and $\mathbf{SDW}_{115}$ are the dry weight of stems (g/plant) at 90 and 115 DAS, respectively.

Assuming that all the P taken up after anthesis was located in the developing ears, the amount of re-mobilized P (RP) in the grains (mg/plant) was calculated as follows:

$$\mathrm{RP} = \mathrm{P}_{\text{grains}} - (\text{Shoot P}_{115} - \text{Shoot P}_{67})$$

RESULTS

In our study, P and water (W) treatments significantly affected plant growth

TABLE 1. Main Stem Leaves Number at 34, 49, and 57 Days After Sowing. Different Letters for Each Date Represent Significant Differences ($P<0.05$).

P Added (µg/g)	Days After Sowing 34	49 Watered	 Stressed	57 Watered	 Stressed
0	4.6b	6.9	6.9	7.9	8.0
15	5.0a	6.9	6.9	8.2	8.4
30	4.8ab	7.4	7.8	8.5	8.6
100	5.0a	7.1	7.8	8.0	8.2

characteristics. Plant development was also impaired by the level of P added, particularly during the first weeks after emergence. The rate of leaf appearance on the main stem was faster when the P supply was increased. This effect was statistically significant at 34 DAS (Tuckey, $P<0.05$) (Table 1). From then on, although high P plants had always more leaves on the main stem, the differences were not significant (Table 1). Furthermore, despite the differences in thermal time until anthesis (Tt) among P or W levels which were not statistically significant, this variable was inversely related to the level of P added ($Tt = 1024 - 1.34 * \text{Added P}$; $R^2 = 0.68^{**}$). A 't' test indicated that the slope of the regression between required thermal time until anthesis and P addition levels was negative and different from zero ($P<0.05$). When no P was supplied, the thermal time required to reach anthesis was 10 and 7% longer with respect to the P100 plants, for the well-watered and drought-stressed plants, respectively. Because of these diferences and as all the plants yellowed at the same time (after about 1,800 degree days), the duration of the grain filling period was probably reduced in the low P plants.

Phopshorus shortage reduced stem and leaf dry matter accumulation, particularly during the early stages of plant growth, in both the well-watered and drought-stressed plants (Figure 1a and b). Afterwards, the differences between the P0 and P100 plants seemed to remain constant. At final harvest (115 DAS), significant interactions between the P and W treatments were observed for leaf and stem dry weight. For these variables, the effect of the drought-stress treatment was

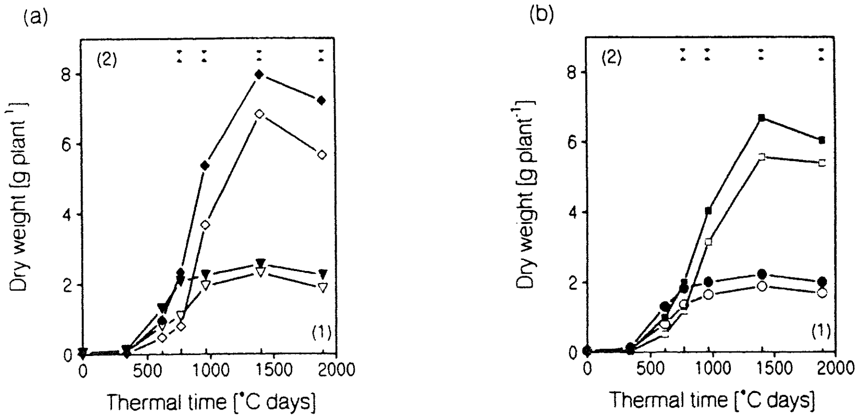

Figure 1. Dry weight of leaves P0 (∇ , ○), and P100 (▼ , ●), and stems P0 (◊ , □), and P 100 (♦ , ■), in well watered (a) and drought stressed (b) plants versus cummulated thermal time after emergence. Bars are standard errors for leaves (1), and stems (2).

larger at the intermediate levels of P supply, P15 and P30 (Table 2). The interactions observed in this study were thoroughly studied in a previous paper (16).

Generaly, the final shoot dry weight and P uptake increased with the level of P supply. The drought-stress treatment had little effect on dry weight and P content, (Table 2). At final harvest, the well-watered plants produced on average, 12.7% more shoot dry matter and absorbed 17.9% more P. With respect to P100 plants, the reduction in grain yield in the P0 plants accounted for about 50% of the total reduction in shoot dry weight in both well-watered and drought-stressed plants. With respect to the P100 plants, the reducton in stem dry weight of the P0 plants accounted for 30 and 7.6% of the total reduction in the well-watered and drought-stressed plants, respectively. Finaly, the reduction in leaf dry weight explained 7.0 and 9.0% of the decrease in shoot dry weight and the decrease in chaff dry weight a 13 and 16.4% for the well-watered and drought-stresses plants, respectively.

At maturity (115 DAS), the addition of 100 μg P/g soil increased shoot P content with respect to the P0 plants by a 59.6 and 37.2% in the well-watered and drought-stressed plants, respectively. In both cases, almost 90% of the increase in shoot P uptake was accounted for a higher P content in the grain (Table 2).

TABLE 2. Dry Weight and P Content of Shoot and Different Organs at Final Harvest (115 DAS). Different Letters Indicated Significant Differences (p<0.05) by a LSD Test. * and ** Indicate Significant Interactions P < 5% and 1%, respectively.

	Watered	Stressed	Watered	Stressed
P Added (µg/g)	**Leaf Dry Weight*** (g/plant)		**Leaf P Content** (mg/plant)	
0	1.86bc	1.69c	0.62e	0.49f
15	2.36a	1.83bc	0.90bc	0.63ef
30	2.22a	1.84bc	0.82cd	0.68de
100	2.24a	2.00b	1.08a	1.06a
	Stem Dry Weight** (g/plant)		**Stem P Content** (mg/plant)	
0	5.6 bc	5.39 c	1.11 b	1.07 b
15	7.3a	5.6bc	1.25b	1.15b
30	7.0a	5.9b	1.45a	1.48b
100	7.2a	6.0b	1.95a	1.44b
	Chaff Dry Weight (g/plant)		**Chaff P Content** (mg/plant)	
0	2.28bc	2.22bc	1.29bc	1.12bc
15	3.52a	2.29bc	1.87ab	1.09bc
30	1.90c	2.55bc	1.53abc	1.08c
100	2.98ab	2.80 ab	2.16a	1.69ab
	Grain Dry Weight (g/plant)		**Grain P Content** (mg/plant)	
0	9.8 bcd	9.21d	33.85cd	31.31d
15	10.8abcd	9.42cd	40.04bcd	34.06cd
30	11.5ab	10.90abcd	44.89ab	35.79bcd
100	12.4a	11.13abc	53.66a	42.46bc
	Shoot Dry Weight (g/plant)		**Shoot P Content** (mg/plant)	
0	19.67c	18.53c	36.88cd	34.00d
15	24.08ab	19.20c	44.08bc	39.65cd
30	22.6abc	21.14abc	48.07b	39.04bcd
100	24.84a	21.98abc	58.87a	46.67b

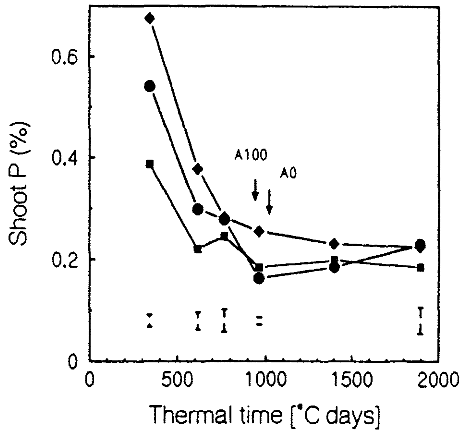

Figure 2. Shoot P (%) concentration in P0 (■), P30 (●) and P100 (♦) plants versus cumulated thermal time. Averaged values for well watered and drought stressed treatments. Bars are standard errors, and arrows indicate anthesis for P0 and P100 plants.

Shoot P concentration decreased with time for all the P treatments and was not affected by water stress (Fig. 2). Phosphorus concentration in shoots of the P0 plants remained constant after 57 DAS (766 cumulated degree days). Phosphorus concentration of P100 plants continued decreasing until 90 DAS (1,400 degree days), and at this time, these plants had almost the same P concentration as the P0 plants. For all the P and W treatments, shoot P concentration was not further reduced after the plants reached a value of 0.2%.

Dry matter as well as P allocation to different shoot organs were affected by P supply, particulary during the early stages of plant development (Fig. 3). Water stress did not affect significantly DMA and PA. DMA to leaves always declined with thermal time, DMA for stems first increased until around anthesis and then decreased. Values for the allocation coefficient lower than 0 were due to re-mobilization of previously accumulated dry weight or P. Allocation to leaves was more important than to stems only before 57 DAS.

Net re-mobilization of P from leaves and stems started earlier than net re-mobilization of dry matter (Fig. 3a and b). Net export of dry matter from leaves and stems was observed after 90 DAS, whereas net export of P started at 67 DAS

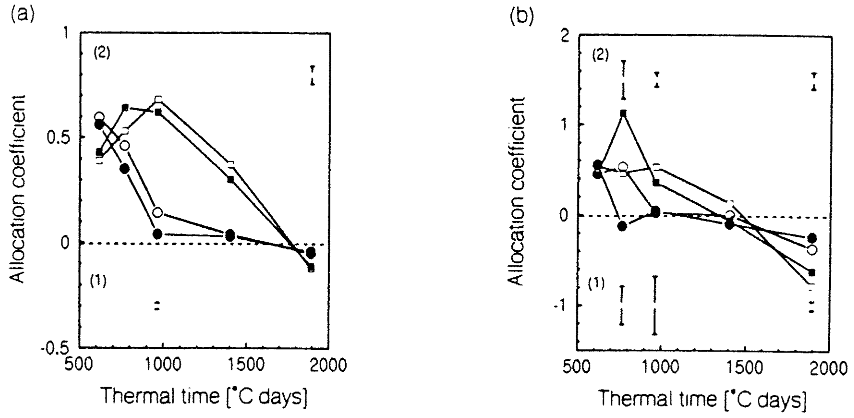

Figure 3. Allocation coefficients for dry matter (a), and phosphorus (b), in leaves P0 (O) and P100 (●), stems P0 (□) and P100 (■), versus cumulated thermal time. Averaged values for well watered and drought stressed treatments. Bars are standard errors for leaves (1), and stems (2).

(964.7 degree days). Net export of P and dry matter started earlier in high-P plants than in low-P plants (Fig. 3b), presumibly because sink formation had been strongly stimulated.

Before the period of net export had started (anthesis), P and dry matter were accumulated in similar proportions (1:1 for the allocation coefficients) in leaves and stems (Fig. 4a and b). In stems before anthesis, allocation of dry matter and P first increased and then decreased falling on all the points on the 1:1 line (Fig. 4b). After anthesis, net export of dry matter and P were observed from leaves and stems. Dry matter and P were exported in a constant proportion, but smaller than 1. For each unit in allocation of P out of leaves, the allocation of dry matter was 0.34, and in the stems, the ratio was 1:0.60. These figures show that, in relative terms, P was more labile for reallocation than dry matter.

Phosphorus and dry matter were accumulated in the ear in a constant proportion with respect to time (Fig. 4c.). However at higher levels of P supply, the amount of dry matter per unit of P accumulated into the ears was smaller (Fig. 4c). For simplicity, as shown in Figure 4c, only the P0 and P100 treatments for the well-watered and drought-stressed plants were included. According to a "F" test

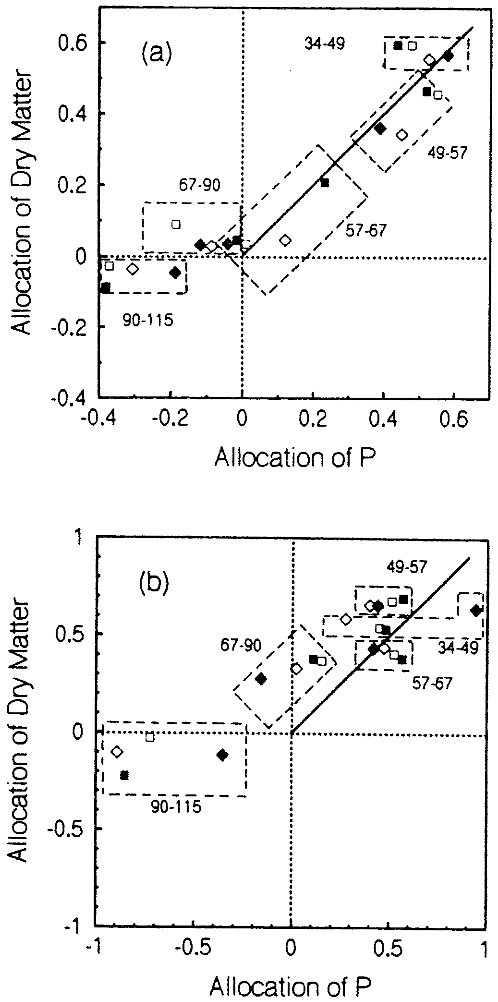

Figure 4. Allocation coefficients for dry matter versus allocation coefficients for phosphorus, in leaves (a), and stems, and accumulation of dry matter versus accumulation of P in ear (c). Simbols are means, P0 well watered (■), P0 drought stressed (□), P100 well watered (⧫) and P100 drought stressed (◊) plants.

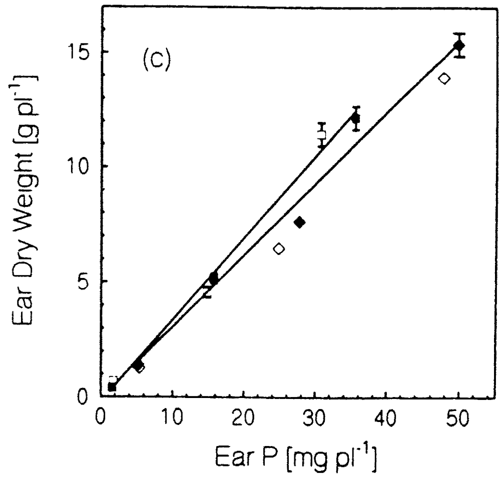

Figure 4 Continued

(P<0.05), the slopes of the regression lines in Figure 4c were different. Irrespective the watering treatment, for each miligram of P accumulated in the ear, 357 and 308 mg of dry weight were allocated into the ear for the P0 and P100 plants, respectivelly.

As leaf and stem dry weight continued increasing until 90 DAS (Fig. 1a and b), the export of dry matter from the leaves and stems to the ears was calculated assuming that before 90 DAS re-mobilization was negligible. Neither the P nor drought-stress treatments affected the proportion of dry matter re-mobilized from different organs to the ear. At final harvest, only a 8.22% (CV = 37%) of the ear dry weight originated from re-mobilized materials. Most of the re-mobilized dry matter in ears cames from the stems, about 72.2%.

RP increased with the level of P addition (Table 3). Drought-stressed plants had lower re-mobilization to the ears than well-watered plants, though the differences were not statistically significant (Table 3). The proportion of re-mobilized P was found linearly related to the final number of grains per plant (a measure of the sink strength) (Fig. 5).

DISCUSSION

For wheat, temperature, photoperiod, and vernalization (despite genetic variation and developmental stages) are known to be the main factors influencing

TABLE 3. Remobilized P, and Proportion of P Remobilized in Grains. LSD for RP was 9.3 mg/plant, and for the Proportion of RP in Grains was 22.8.

P Added (µ/g)	Remobilized P (mg/plant)		Proportion of Remobilized P (%)	
	Watered	Stressed	Watered	Stressed
0	7.54c	8.00bc	22.20a	22.90a
15	12.2abc	6.97c	30.24a	20.40a
30	14.97abc	7.60c	30.40a	20.80a
100	21.14a	17.06ab	39.10a	40.04a

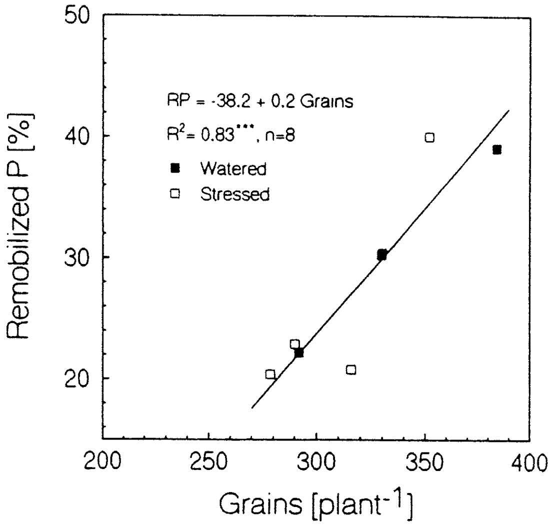

Figure 5. Remobilized P (%) versus number of grains per plant in well watered (■) and drought stressed (□) plants.

the rate of plant development (17). However, plant mineral nutrition can influence development. Gregory et al. (3) found that the addition of both N and P, or P alone, changed the development of barley by advancing the time to anthesis and maturity.

Rodriguez et al. (2) found that the duration of the phyllochron on wheat plants growing in two different soils was inversely related to the concentration of P in the shoots early during plant development. Hajabbasi and Schumacher (18) also showed that the addition of P decreased the time to reach a given developmental stage for two genotypes of maize. In our study, and in coincidence with previous reports, we observed that the development of wheat plants, though not statistically significant, was slightly impaired when they were grown in a low P mixture of soil and sand. Plant development until anthesis was delayed in the P0 plants by 10 and 7% with respect to the P100 plants for well-watered and water-stressed plants, respectively. Furthermore, the initial rate of main stem leaf tip appearance was delayed when no P was supplied. These results also suggest that any delay in development due to P deficiency before anthesis, as mentioned by Squire (4), would be compensated afterwards with a shorter grain filling period. In our study, we found that low P delayed anthesis, and although physiological maturity was not determined, all the plants yellowed at the same time.

When examining the way in which source-sink relationships regulate partitioning of C in plants, consideration must be given to the timing of organ initiation and development. The latter controls both the overlap in the growth of competing sinks as well as the relationship between photosynthetic sources and growing sinks (5). We found that the allocation of dry matter among different plant organs was significantly affected by the level of P supply. It has already been mentioned that plant development until anthesis was delayed in the P0 plants by 10 and 7% for well-watered and water-stressed plants, respectively, this delay being of the same magnitude as that observed in the allocation coefficients for dry weight into the different plant organs (see Figure 3a). The effect of P on dry matter allocation was apparently driven by the effects of P deficiency on the developmental state of the plants at the time of each harvest.

In most agronomic models for crop growth and production under sufficient P conditions, dry matter allocation depends on plant development (19). However, many models that intend to simulate the effects of P nutrition on plant growth do not contemplate the effects of P nutrition on plant development or dry matter allocation among aerial organs (20,21). Although computer modelling requires categorization and simplification, the degree to which the modelling is successful depends on how well the major factors are defined (17). Central to this is the understanding of the movement of captured resources (carbohydrates, nutrients, and water) between different parts of the plant, and their role in regulating dry matter accumulation. Our lack of knowledge of the mechanisms governing allocation is one of the main limits to the development of process-based models for whole plants (11). We have shown in this study that even when the effects of P deficiency on plant development were mild, dry matter allocation into aerial organs was significantly impaired. Therefore, in any modelling attempt of plant growth and production under P-limiting conditions, an accurate description of plant development and dry matter allocation will be crucial.

The P and N transferred to the ear are supplied from two distinct sources, post anthesis uptake from the soil and internal redistribution of nutrients and carbohydrates accumulated by leaves and other parts of the plant during the early stages of growth. Under low-P conditions, redistribution of P and dry matter was mentioned to play an important role in grain filling (14). In this study, although most of the P accumulated by the ear originated from post-anthesis uptake, the ratio of carbohydrates and P exported from the leaves and stems was influenced by the final composition of the grains. Our results suggest a lack of synchronization between the requirement of P and dry matter by the ear. Also, we found that net re-mobilization of P preceded net re-mobilization of dry matter, and the P100 plants started the re-mobilization of P from leaves and stems earlier than the P0 plants. This was associated with an earlier and probably stronger sink formation in the P100 plants respect to the P0 plants. Furthermore, accumulation of dry matter and P in the growing ear was different at different levels of P supply. At a higher P availability, less dry matter was accumulated by the ear per unit of P. This supports the hypothesis that P and carbohydrates accumulation by the ear is independently regulated. Evidences of lack of interdependence between C and N (22,23), and C and P (14,24) have been also reported by others.

In this experiment, there were no differences among treatments in the proportion to the re-translocated of P (PRP, %) in the grain. Additionally, the values of PRP were similar to those found by Batten et al. (12) in high-P plants. Batten et al. (12), found that high-P plants derived 21% of their grain P from shoot tissue, while in low-P plants, the amount derived from re-mobilization varied with experimental conditions but ranged from 51 to 89%. In this experiment, P re-mobilization was observed to be more related to the strength of the sink than to P or water limitation. The higher the grain numbers per plant, the higher the P reallocation towards the ears. Several times it has been indicated, that in order to rise yields, significant reductions in the export of P by low-P plants are necessary to slow senescence that is induced by P deficiency, while extening the photosynthetic leaf area duration. However, the extent of such a concept seems to dependent on the severity of the P limitation. In our study, the degree of P deficiency was mild and similar to that observed under field conditions, and therefore, the extent of P re-mobilization in the low-P plants was low probably due to a smaller grain number per plant, a variable defined relatively early during the development of the plants. It is important to mention here, that the water-stress treatment did not have any effect on these attributes.

In this study, plants growing at different levels of P and water supply presented a different developmental state at each harvest. The effects of P or water supply on plant development affected the timing of dry matter allocation to different aerial organs. Low-P plants were delayed in development and also allocation was delayed. The water-stress treatment had little effect on plant development and therefore, changed allocation very little. The final composition of the grains was dependent on the re-mobilized of materials from other plant organs, and the proportion of carbohydrates and P re-mobilized seemed to be independent.

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