Kasetsart J. (Nat. Sci.) 48 : 348 - 363 (2014)

Dynamics of Assimilate Translocation and Its Contribution to Maize Kernel Exposed to Different Periods of Water Deficit

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ABSTRACT

Field experiment I was conducted under moderate water deficit conditions at four different growth stages (V10 to V13, V13 to V17, V17 to blister and blister to physiological stage) with three maize genotypes (Pioneer 30B80, NK 40 and Suwan 4452) and field experiment II was conducted under severe water deficit conditions at three stages (V10 to anthesis, anthesis to milk and milk to physiological maturity stage) with two genotypes (NK 40 and Suwan 4452) to evaluate the hypothesis that the translocation of stored stem reserves into the growing grain is an important source of carbon for supporting grain filling under water deficit. Significantly higher assimilate translocation, assimilate translocation efficiency and contribution of pre-anthesis assimilates to the grain were achieved in the V17 to blister stage under moderate water deficit and in the milk to physiological maturity stage under severe water deficit, respectively, with maximum stem dry weight depletion and stem dry weight depletion coefficients. NK 40 always sustained a smaller reduction in grain weight under both experiments. During grain filling, NK 40 exported 43.51 and 28.38% higher stem reserve dry matter compared to Pioneer 30B80 and Suwan 4452 under moderate water deficit conditions and a 46.20% higher stem reserve contribution compared to Suwan 4452 under severe water deficit conditions. Assimilate translocation in the two experiments showed a significant positive relationship with stem dry weight depletion (R^2 = 0.81 and 87, respectively) and specific leaf weight depletion (R^2 = 0.93 and 88, respectively), whereas it showed a significant negative relationship with the source-sink ratio (R^2 = -0.53 and -0.84, respectively) and chlorophyll content (R^2 = -0.50 and -0.63, respectively).

Keywords: water deficits, maize genotypes, stem weight depletion, assimilate translocation, assimilate contribution, grain filling

INTRODUCTION

Maize is extensively grown in temperate, subtropical and tropical regions of the world (Muchow, 1989). The productivity of maize is not just due to the accumulation of dry matter, but depends also on its effective partitioning to plant parts of economic importance which is a key to yield stability. During grain filling, the occurrence of different biotic and abiotic stress factors, such as water deficit, decreases photosynthesis (Bdukli *et al*., 2007). Under water stress conditions, stem accumulation increases and remobilization of stem reserves is an important supporting process that can largely compensate for grain yield decrease (Palta *et al*., 1994). Leaf photosynthesis is also decreased

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Received date : 02/10/13 Accepted date : 17/12/13

by various stresses such as drought, heat stress and leaf diseases (Bdukli *et al*., 2007) resulting in grain filling becoming largely dependent on vegetative sources and photosynthesis of ear tissue (Paponov *et al*., 2005). Remobilization of reserves in the grain is critical for grain yield if the plants are subjected to water stress during grain filling (Palta *et al*., 1994). Among cereals and particularly in corn, pre-anthesis assimilates increase the yield stability during terminal drought stress (Blum *et al*., 1983). In wheat, pre-anthesis assimilate reserves in the sheath contribute 25-33% of the final grain weight (Gallagher *et al*., 1976; Hans 1993; Gebbing *et al*., 1999). In cereals, grains are the most important sink for carbon and nitrogen after anthesis; pre-anthesis storage may contribute 20-40% of the final crop yield depending on the cultivar, reflecting its importance in attaining higher grain yields (Yoshida, 1972). One way to achieve reasonable yield is to assess the remobilization rate of carbohydrates and proteins that are produced under stressful conditions and considered as an effective physiological index of eventual yield.

Genetic variation in assimilation and remobilization under drought stress has been reported in some studies (Royo and Blanco, 1999; Álvaroa *et al*., 2008; Ehdaie *et al*., 2007). A simple and effective method for determining the amount of remobilized dry matter is to measure differences in stem dry weight between the anthesis and maturity stages (Ehdaie *et al*., 2007). A better understanding of the performance of maize genotypes in terms of dry matter accumulation and translocation of photosynthetic assimilates under field capacity soil water and water deficit condition will assist in selecting new genotypes, suitable for cultivation in drought prone areas.

The aim of this study was to evaluate some physiological parameters of maize genotypes—assimilate translocation, assimilate translocation efficiency, contribution of pre and post-anthesis assimilate to maize grain—along with the depletion of reserved dry matter from vegetative plant organs under control (well watered) and water deficit conditions induced at different growth and development stages.

MATERIALS AND METHODS

Set up field experiment

Two field experiments were carried out at the National Corn and Sorghum Research Center (latitude 14.5^{0}N, longitude 101^{0}E 360 m above sea level) located in Pak Chong, Nakhon Ratchasima, Thailand during the 2010-2011 and 2011-2012 growing seasons. A split plot arrangement based on a randomized complete block design with three replications was used. For experiment I, the main plots consisted of five water regimes—D1 (control-soil water status maintained near field capacity), D2 (water deficit from V10 to V13 stage, 42–56 d after planting), D3 (water deficit from V13 to V17 stage, 57–71 d after planting), D4 (water deficit from V17 to blister stage, 72–86 d after planting) and D5 (water deficit from blister to physiological maturity stage). Three hybrid field corn genotypes—Pioneer 30B80, NK 40 and Suwan 4452—were selected as subplots.

For experiment II, four water regimes—D1 (control-soil water status maintained near field capacity), D2 (water deficit from V10 to anthesis), D3 (water deficit from anthesis to milk stage) and D4 (water deficit from milk to physiology maturity stage)—were applied as the main factor and the two best genotypes from experiment I—namely, NK 40 and Suwan 4452—were selected as subplots.

The experimental field was fertilized with mixed fertilizer (N:P =16:20) at the rate of 156 kg.ha^{-1} during final land preparation. The same amounts of mixed fertilizer were applied as top dressing during the 8–10 leaf stage. The seeds of each maize genotype were sown using a manual planting machine with two seeds per hill in 10 rows in each plot 7.5 m long, with a spacing of 75 cm and 25 cm between rows and plants, respectively. The day after seed planting, sprinkler irrigation was applied to the plots for better germination of seeds and thereafter irrigation was continued at weekly intervals until the maize plants reached the knee-high stage. The plants were thinned at the 4-leaf stage to maintain one plant per hill. Five plants were randomly selected from each plot and cut at the soil surface at the anthesis and maturity stages. The plants were separated into stems, leaves and ears at each stage. After initial sun drying for 3-4 d, the samples were dried in an oven at 60°C for 72 hr.

Physiological parameter measurement

Different parameters describing the assimilate mobilization and translocation within the plant were calculated according to Arduini *et al*. (2006), Dordas *et al*. (2008), Jiang *et al*. (2008) and Singh (2011) as follows:

AT = DMSa - DMSm

ATE = (AT/DMSa) × 100

CPAA = (AT/GY) × 100

CCA = CAT/GY × 100

SWD = (Max DW- DWm)

SWDC = SDW/Max DW × 100

where AT is the assimilate translocation (grams per plant), DMSa is the dry matter shoot at anthesis, DMSm is dry matter shoot at maturity (leaf + culm + chaff), ATE is the assimilate translocation efficiency (%), CPAA is the contribution of pre-anthesis assimilates to grain (%), GY is the grain yield (grams per plant), CCA is the contribution of current assimilate, CAT is the current assimilate translocation, SWD is the stem dry weight depletion (grams per culm), Max is an abbreviation of maximum, DW is the dry weight (grams), DWm is the dry weight at maturity (grams) and SWDC is the stem dry weight depletion co-efficient.

For the assimilate translocation estimates, it was assumed that all of the dry matter lost from vegetative plant parts was translocated to the developing grain, since losses of dry matter due to plant respiration during grain filling were not determined.

Statistical analysis

Data on different parameters were analyzed using analysis of variance which was performed with the MSTATC software (Version 1.2; Michigan State University, MI, USA). The significant differences between treatment means were compared with the critical difference at the 5% probability level using Duncan's multiple range test.

RESULTS AND DISCUSSION

Water deficit response on assimilate translocation parameters (experiments I and II)

For experiment I, Figures 1a, 1b, 1c, 1d, 1e and 1f show the depletion of stem dry weight (SWD), dry weight depletion co-efficient (SWDC), assimilate translocation (AT), assimilate translocation efficiency (ATE), contribution of pre-anthesis assimilate to grain (CPAA) and contribution of current assimilate to grain (CCA), respectively. These traits were measured between anthesis and the end of grain filling. The respiration rate was negligible compared with remobilization; the change of stem dry weight is a good estimate of the amount of water-soluble carbohydrates remobilized during grain filling (Ehdaie *et al*., 2008). The stem dry weight depletion and dry weight depletion co-efficient varied under different water deficit treatments. The stem dry weight depletion ranged from 3.13 to 10.36 g per culm under water deficit conditions. The dry weight depletion co-efficient varied from 5.51 to 17.2%. The maximum depletion of the stem dry weight and the dry weight depletion co-efficient occurred in the D4 (V17 to blister stage) treatment while the well-watered treatment exhibited the lowest dry weight depletion and dry weight depletion co-efficient. This result indicated that the water deficit in the D4 treatment enhanced maximum transportation of the stored assimilates in the stem to the maize kernel in response to plant growth. After reaching its maximum dry matter content, the stem dry weight started to decline from grain

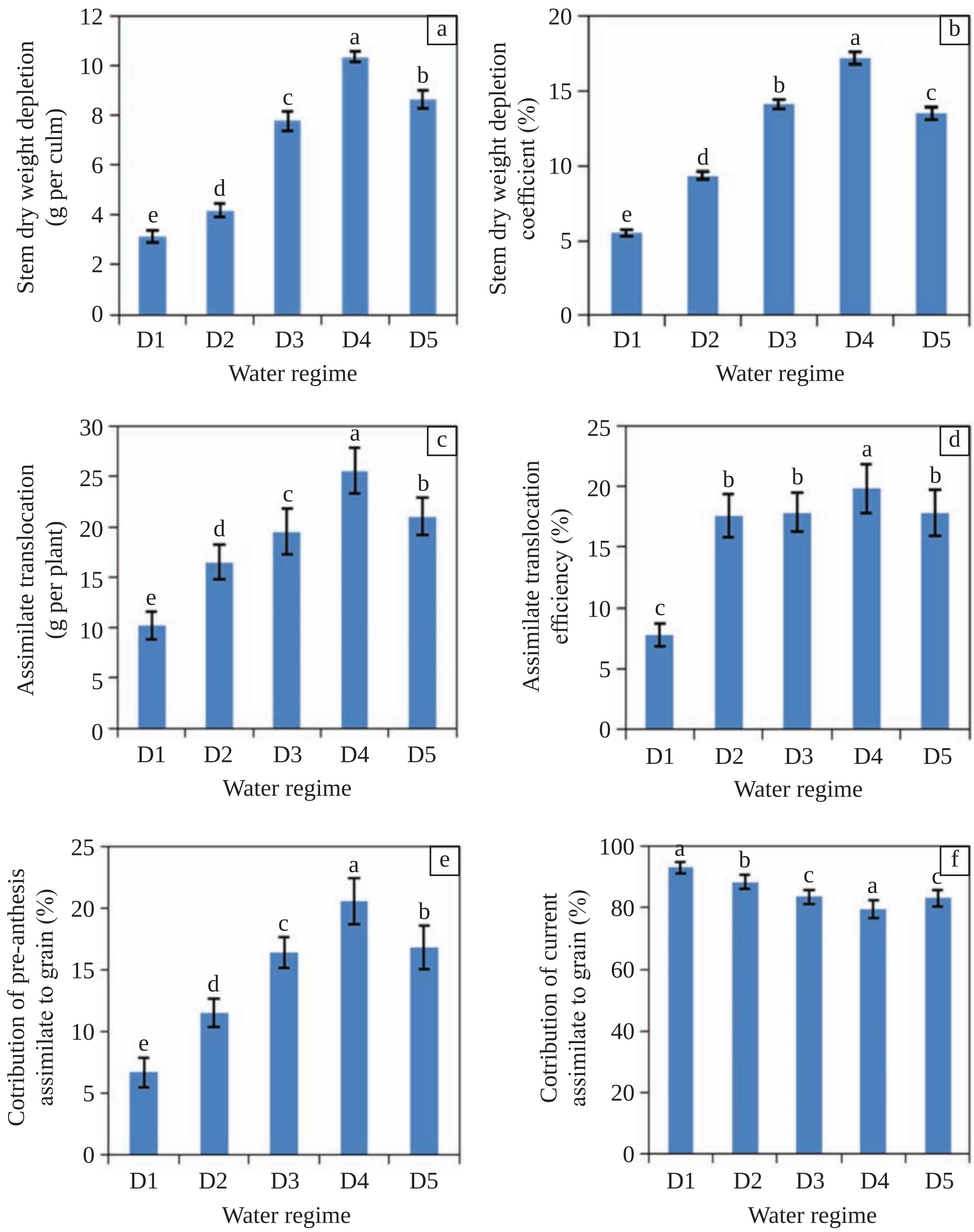

Figure 1 Effect of water regimes in experiment I on: (a) Stem dry weight depletion; (b) Stem dry weight depletion coefficient; (c) Assimilate translocation; (d) Assimilate translocation efficiency; (e) Contribution of pre-anthesis assimilate to grain; (f) Contribution of current assimilate to grain of maize. D1 = Field capacity (control), D2 = Water deficit from V10 to V13, D3 = Water deficit from V13 to V17, D4 = Water deficit from V17 to blister, D5 = Water deficit from blister to physiological maturity. Vertical bars indicate the standard deviation of the means and the letters above the bars indicate significant differences at $P \leq 0.05$.

filling to physiological maturity indicating that assimilates had moved to the grains. However, it has been suggested that water deficit itself does not increase the remobilization, but environmental conditions that decrease current photosynthetic assimilation cause a greater requirement on the stem carbohydrate reserves during the grain filling (Rawson *et al.,* 1983).

As shown in Figure 1c, the translocation of pre-anthesis assimilate stored in vegetative organs to grain differed significantly due to the different water deficit conditions. The results demonstrated that assimilate translocation under water deficit conditions was significantly higher than that under well watered conditions. The highest assimilate translocation (25.56 g per plant) was exhibited in the D4 treatment followed by the D5 water deficit treatment. The lowest assimilate (10.2 g per plant) was translocated to grain under the well watered treatment (D1). The highest assimilate translocation observed under D4 (V17 to blister stage) water deficit conditions was in agreement with the results of Behesti and Behfoodi fard (2010) on sorghum genotypes. During grain filling, the occurrence of different biotic and abiotic stress factors (such as water deficit) decreases current photosynthesis (Bdukli *et al.*, 2007) due to the decrease in the leaf stomatal conductance and net CO_2 assimilation for many species (Bradford and Hsiao, 1982). Under this condition, the demand rate for the utilization of stem accumulation increases and translocation of assimilate from the stem reserves becomes the predominant source (Blum *et al*., 1994) contributing to grain filling and largely compensates for any grain yield decrease (Palta *et al*., 1994).

For experiment II, Figures 2a, 2b, 2c, 2d, 2e and 2f represent the SWD, SWDC, AT, ATE, CPAA and CCA, respectively. The stem dry weight depletion and dry weight depletion co-efficient were significantly influenced by severe water deficit treatments (Figures 2a and 2b, respectively). The stem dry weight depletion ranged from 10.01 to 61.5 g per culm under severe water deficit conditions. The dry weight depletion co-efficient varied from 7.01 to 29.65%. The maximum depletion in the stem dry weight and dry weight depletion co-efficient occurred in water stress from the milk to physiological maturity (D4) stage while water deficit from V10 to anthesis resulted in the lowest stem dry weight depletion and dry weight depletion co-efficient. This result indicated that a severe water deficit at the terminal stage greatly enhanced stem reserve degradation and subsequent mobilization to grain.

Figure 2c shows the pattern of assimilate translocation under severe water stress conditions. Assimilate translocation ranged from 9.16 to 38.94 g per plant and indicates that severe water stress during V10 to anthesis stage resulted in the lowest assimilates translocation. The maximum translocation of assimilate was observed under water deficit from the milk to physiological maturity stage. From both experiments the results indicate that the severity and duration of water deficit had a significant influence on stem reserve degradation and translocation to grain. The severity of water stress and the dynamics of assimilate translocation from the vegetative plant parts are dependent on the growth and development stages of maize crop. A moderate water deficit after anthesis (D4) in experiment I accounted for the maximum depletion of stem weight (10.36 g per culm) and other vegetative parts contributed to the maximum translocation of 25.56 g per plant whereas severe water deficit during the milk to physiological stage induced comparatively higher stem weight depletion (61.5 g per culm) and translocation to grain (38.94 g per plant).

Under moderate water deficit (experiment I), the assimilate translocation efficiency (ATE) and the contribution of pre- anthesis assimilates to grain (CPAA) under well watered and water deficit conditions showed significant variations (Figures 1d and 1e). Surprisingly, the application of the different irrigation regimes in the D1 to D5

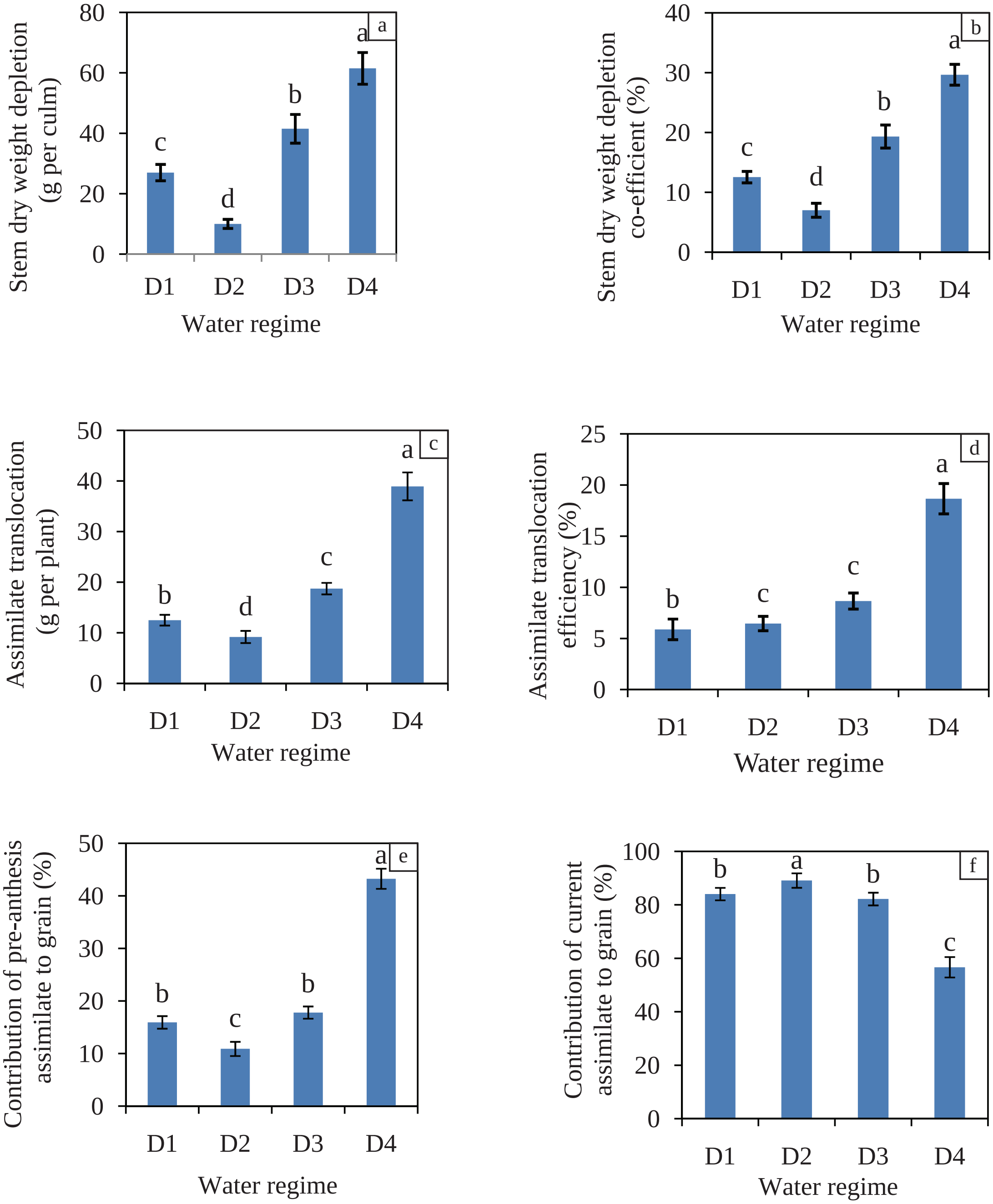

Figure 2 Effect of water regimes in experiment II on: (a) Stem dry weight depletion; (b) Stem dry weight depletion coefficient; (c) Assimilate translocation; (d) Assimilate translocation efficiency; (e) Contribution of pre-anthesis assimilate to grain; (f) Contribution of current assimilate to grain of maize. D1 = Field capacity (control), D2 = Water deficit from V10 to V13, D3 = Water deficit from V13 to V17, D4 = Water deficit from V17 to blister, D5 = Water deficit from blister to physiological maturity. Vertical bars indicate the standard deviation of the means and the letters above the bars indicate significant differences at $P \leq 0.05$.

treatments increased the contribution of the CPAA. The CPAA was 6.72% under well-watered (D1) conditions and increased to 20.57% under water deficit conditions during the early grain filling period (V17 to blister stage). It has been reported that a rapid decrease in canopy photosynthesis after anthesis, under terminal drought conditions, caused a reduction in the contribution of current assimilates to grain filling (Ehdaie *et al.*, 2006). Consequently, a considerable amount of stem-reserved carbohydrates are translocated to grains during the grain filling period (Rawson and Evans, 1971; Gent, 1994). The increase in CPAA observed in the present study was in agreement with the above reports. The pattern of changes in ATE and CPAA was consistent with the depletion of the stem dry weight and dry weight depletion co-efficient.

Under severe stress (experiment II), ATE and CPAA were affected significantly by the water regimes. The control conditions produced the lowest translocation efficiency (ATE) and the maximum efficiency of dry matter translocation was recorded during the milk to physiological stage. The contribution of pre-anthesis assimilate to grain followed the same pattern as the SWD, SWDC and AT (Figures 2d and 2e).

In experiment I, water deficit induced considerable changes in the contribution of CCA (Figure 1f). The maximum value of this trait was recorded under well watered (control) conditions, while the minimum value of CCA was in the D4 treatment. The possibly limited photosynthesis due to less CO_2 acquisition through stomata under water deficit conditions might have been the reason for the lower current assimilates mobilization and contribution to the maize grain. In experiment II, the maximum CCA was found in the D2 (V10 to anthesis) treatment and the minimum CCA occurred in D4 (milk to physiological maturity).

Relationship between soil water depletion and physiological parameters (experiments I and II)

The stem dry weight depletion under both experiments showed a relatively lower positive relationship (R^2 = 0.42 and 0.33 for experiments I and II, respectively) with the soil water depletion but the upward trend indicated that the stem dry weight depletion occurred under soil water depletion (Figures 3a and 4a, respectively). It also indicated that in experiments I and II, the specific leaf weight depletion had a markedly higher positive relationship (R^2 = 0.61 and 0.77, respectively) with soil water depletion (Figures 3b and 4b, respectively).

Relationship between translocation parameters (Experiments I and II)

For both experiments I and II, assimilate

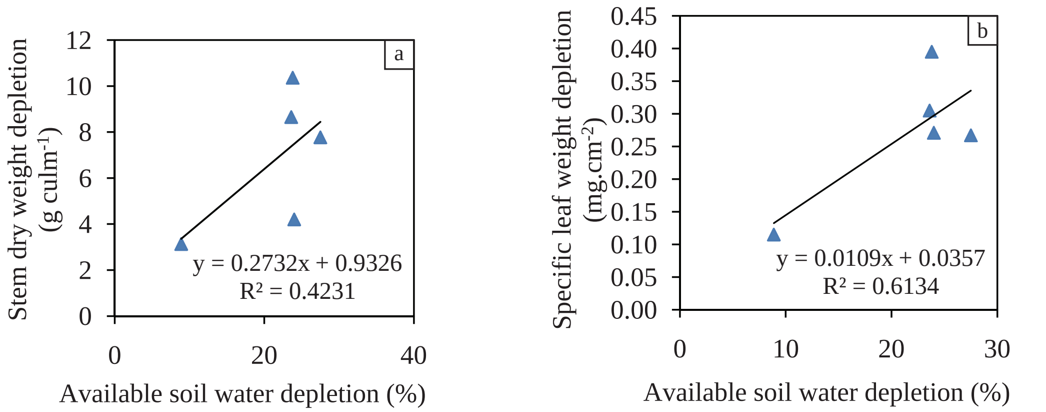

Figure 3 Relationship of available soil water depletion in experiment I with: (a) Stem dry weight depletion; (b) Specific leaf weight depletion.

translocation showed a strong positive relationship with the stem dry weight depletion (R^2 = 0.81 and 0.87, respectively) and with specific leaf weight depletion (R^2 = 0.93 and 0.88, respectively), whereas it showed a relatively weaker negative relationship with the source-sink ratio under the moderate water deficit (R^2 = - 0.53) and a strong negative relationship under the severe water deficit (-0.84). A relatively lower weaker relationship was found between assimilate translocation and chlorophyll content under the moderate water deficit whereas a stronger negative relationship was observed under the severe water deficit (R^2 = -0.50 and -0.63, respectively) as shown in Figures 5 and 6).

Genotypic response on assimilate translocation parameters (experiments I and II)

In experiment I, there were significant differences among maize genotypes for assimilate translocation. The maize genotype NK 40 exhibited the highest AT of 27.02 g per plant compared to the genotypes Pioneer 30B80 and Suwan 4452 which showed AT values of 13.21 and 15.44 g per plant, respectively (Table 1). The highest stem dry weight depletion and stem dry weight depletion coefficient were also noted in NK 40. This result indicated that significant genetic variation exists for SWD, SWDC and AT among the maize cultivars. Ehdaie *et al*. (2007) reported that assimilate translocation and other associated traits are influenced by genetic and environmental factors. In experiment II, genotypes exposed to severe water deficit also significantly varied with respect to translocation traits. NK 40 showed higher SWD, SWDC and AT compared to Suwan 4452 (Table 2). The stem weight depletion and depletion co-efficient were remarkably higher under severe water stress compared to moderate water stress conditions but the rate of assimilate translocation was not markedly changed. There was little genotypic response demonstrated in either the stem weight depletion or the coefficient even under the control conditions. This was probably due to seasonal variation resulting from the delayed planting of crops in experiment II. Considering both field trials, NK 40 was promising for its productive capacity and remobilization characteristics under severe water deficit conditions.

The effects of genotype on the assimilate translocation efficiency (ATE) and the contribution of pre-anthesis assimilates to grain (CPAA) in experiment I are shown in Table 1, which indicates that NK 40 recorded the highest values amongst all the genotypes studied. Genotypic differences in ATE and CPAA values have been reported among sorghum genotypes and bread wheat cultivars, similar to the results of the present study (Ehdaie *et*

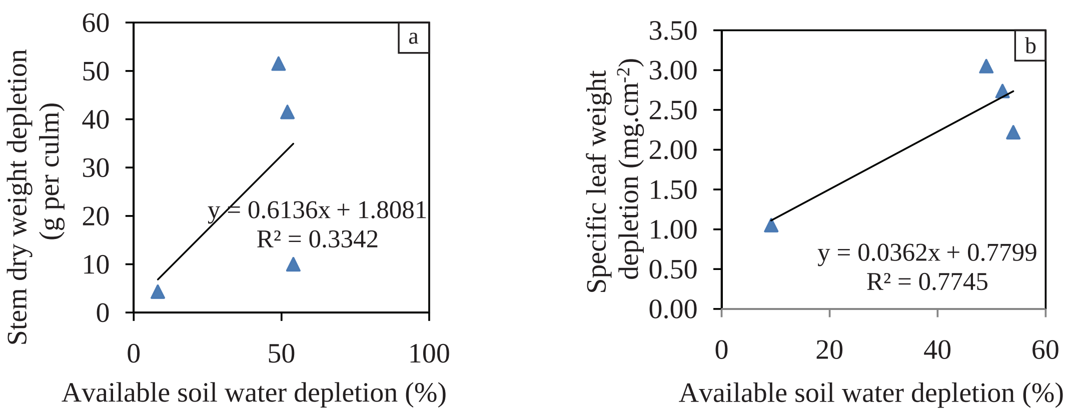

Figure 4 Relationship of available soil water depletion in experiment II with: (a) Stem dry weight depletion; (b) Specific leaf weight depletion.

al., 2008; Inoue *et al.*, 2004; Alvaroa *et al.*, 2008). In wheat, genotypic variation has been found with regard to translocation efficiency (Blum *et al.* 1991, Regan *et al.* 1993, Ehdaie and Waines 1996) though the environmental conditions significantly affect the ability of genotypes to remobilize the stored assimilates. Likewise other traits, ATE (12.69%) and CPAA (28.67%) were also higher in NK 40 compared to Suwan 4452 (7.14 and 15.29%, respectively) under severe stress as shown in Table 2 (experiment II). Furthermore, ATE was higher under moderate water deficit conditions in experiment I whereas CPAA was generally higher under the severe water deficit conditions in experiment II.

Maize genotype also produced significant variation in the contribution of current assimilate (CCA) in experiment 1. Pioneer 30B80 produced the highest CCA to grain (89.29%) followed by Suwan 4452 (86.42%) whereas NK 40 had the lowest value of this trait (81.04%) as shown in Table 1. In experiment II, there was a significantly lower CCA (71.33%) in NK 40 compared to Suwan 4452 (84.71%) as shown in Table 2. The severe water deficit in experiment II enhanced leaf senescence which reduced current photosynthesis.

Interaction effect of water deficit and genotype on translocation traits (experiments I and II)

In experiment I, the interaction effect

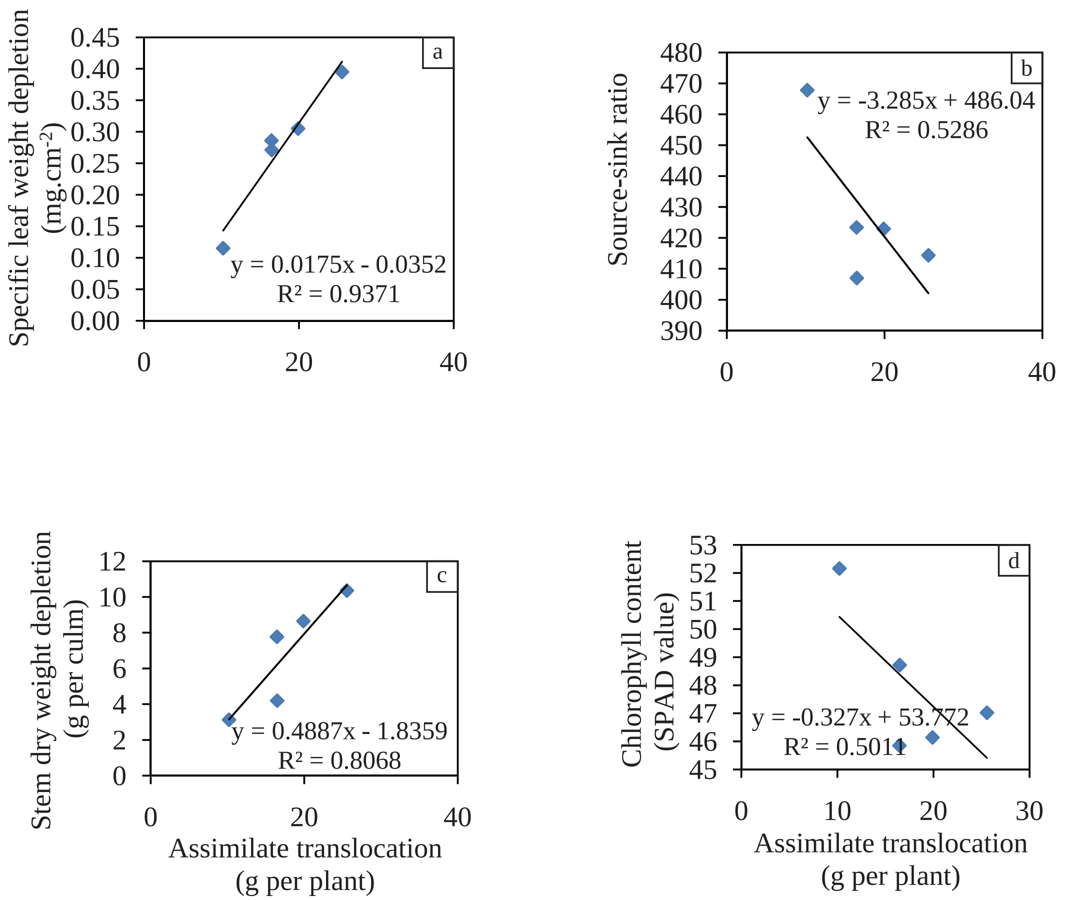

Figure 5 Relationships of assimilate translocation in experiment I with: (a) Specific leaf weight depletion; (b) Source-sink ratio; (c) Stem dry weight depletion; (d) Chlorophyll content. SPAD = Soil and plant analysis development.

of genotype and water deficit on the stem dry weight depletion (SWD), stem weight depletion co-efficient (SWDC), assimilate translocation (AT), assimilate translocation efficiency (ATE) and contribution of pre-anthesis assimilate to grain (CPAA) exhibited similar trends (Table 3). The genotype NK 40 showed the highest AT after anthesis under the D4 and D5 water deficit conditions. The same variety also had the significantly highest SWD, SWDC, ATE and CPAA under the D4 water deficit conditions followed by D5. The value of AT ranged from 8.54 to 23.11, 11.31 to 36.55 and 10.74 to 20.39 g per plant in Pioneer 30B80, NK 40 and Suwan 4452, respectively. ATE was 6.74 to 12.14%, 9.04 to 29.3% and 7.61 to 18.81% in Pioneer 30B80, NK 40 and Suwan 4452, respectively. Under water deficit conditions, the assimilate translocation efficiency was considerably higher for NK 40 which seemed to have more potential compared to Pioneer 30B80 and Suwan 4452. The lowest values for SWD, SWDC, AT, ATE and CPAA were recorded for Pioneer 30B80 under the well watered conditions.

The results demonstrated that the CPAA increased considerably with increased water deficit during the D2 (V10-V13), D3 (V13-V17) and D4 (V17-blister stage) stages while it decreased slightly during the D5 (blister-physiological maturity) for all the genotypes studied (Table 3). However, surprisingly, the CPAA increased in NK 40 under D4 water deficit conditions compared to the other genotypes. This suggested that the superior characteristics of NK 40 in relation to the

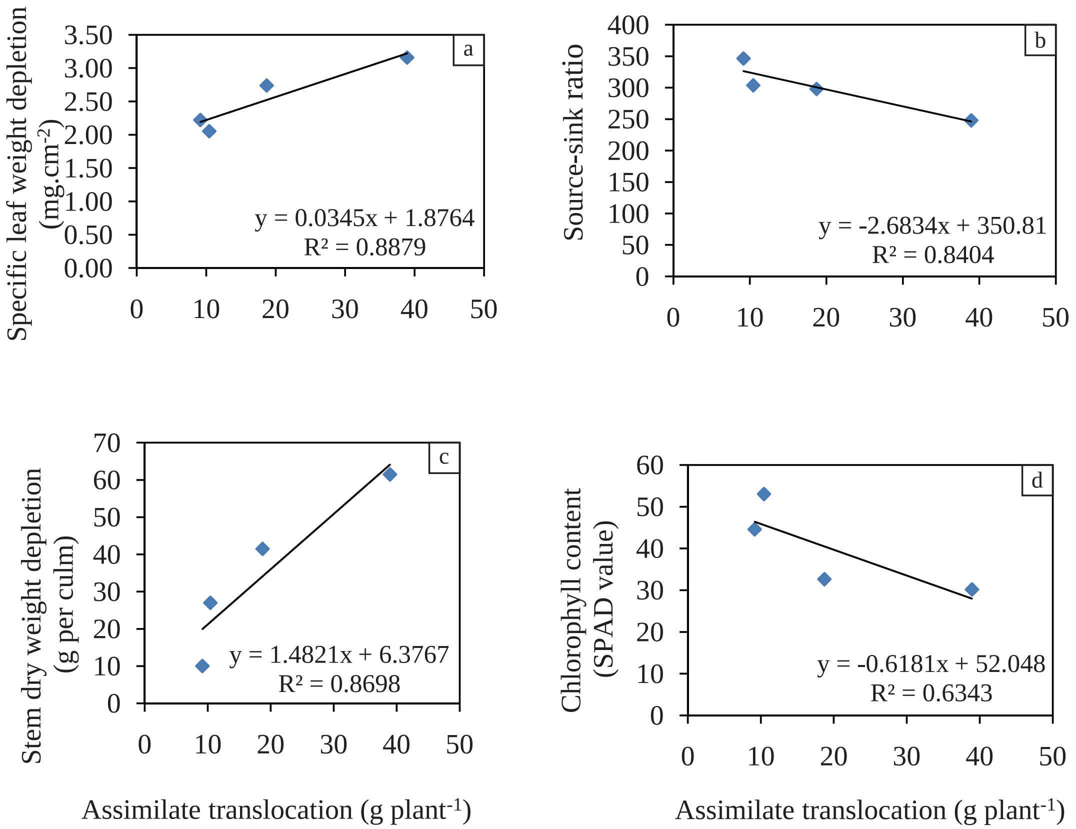

Figure 6 Relationships of assimilate translocation in experiment II with: (a) Specific leaf weight depletion; (b) Source-sink ratio; (c) Stem dry weight depletion; (d) Chlorophyll content. SPAD = Soil and plant analysis development.

remobilization of pre-anthesis assimilates during grain filling makes it a good candidate as a maize drought tolerance genotype in the future. Several researchers have confirmed that the water soluble carbohydrates in stems contribute the main carbon source for grain yield under terminal, limited photosynthetic conditions due to drought stress during grain filling and it has also been introduced as a physiological indicator related to drought tolerance (Ehdaie *et al*., 2007; Diab *et al.*, 2004; Van Herwaarden *et al.*, 2006).

In experiment II, the parameters relating to translocation showed a similar pattern of response. NK 40 showed significantly higher assimilates translocation under water deficit during the milk to physiological stage (D4). The same variety also had the significantly highest SWD, SWDC, ATE and CPAA under the D4 water deficit conditions. The value of AT ranged from 12.96 to 46.96 and from 5.36 to 30.92 g per plant in NK 40 and Suwan 4452, respectively (Table 4). ATE ranged from 7.46 to 20.87% and from 3.64 to 16.45% in NK 40 and Suwan 4452, respectively. The results showed there was significantly higher CPAA at the milk to physiological stage (D4) in both genotypes. However, the CPAA value increased in NK 40

Table 1 Comparison of mean translocation parameters of maize genotypes in experiment I at National Corn and Sorghum Research Center, Pak Chong, Nakhon Ratchasima, Thailand during 2010-11.

Genotype	SWD (g per culm)	SWDC (%)	AT (g per plant)	ATE (%)	CPAA (%)	CCA (%)	GY (kg.ha^{-1})
Pioneer 30B80	5.58^{b}	9.33^{c}	13.21^{c}	11.63^{c}	10.71^{c}	89.29^{a}	7127^{b}
NK 40	9.19^{a}	16.75^{a}	27.02^{a}	22.59^{a}	18.96^{a}	81.04^{c}	7712^{a}
Suwan 4452	5.70^{b}	9.71^{b}	15.44^{b}	14.28^{b}	13.58^{b}	86.42^{b}	7466^{ab}
LSD (*P* = 0.05)	0.15	0.14	1.042	0.85	0.53	0.71	393.70

SWD = Stem weight depletion; SWDC = Stem weight depletion coefficient; AT = Assimilate translocation; ATE = Assimilate translocation efficiency; CPAA = Contribution of pre-anthesis assimilate to grain; CCA = Contribution of current assimilate; GY = Grain yield.

a, b, c = Means in the same column followed by different letters are significantly different at 5% level of probability using Duncan's multiple range test.

LSD = Least significant difference.

Table 2 Comparison of mean translocation parameters of maize genotypes in experiment II at National Corn and Sorghum Research Center, Pak Chong, Nakhon Ratchasima, Thailand during 2011-12.

Genotype	SWD (g per culm)	SWDC (%)	AT (g per plant)	ATE (%)	CPAA (%)	CCA (%)	GY (kg.ha^{-1})
NK 40	46.34	21.34	26.62	12.69	28.67	71.33	6324
Suwan 4452	23.67	12.93	13.03	7.14	15.29	84.71	5868
LSD (*P* = 0.05)	**	*	**	**	**	*	*

SWD = Stem weight depletion; SWDC = Stem weight depletion coefficient; AT = Assimilate translocation; ATE = Assimilate translocation efficiency; CPAA = Contribution of pre-anthesis assimilate to grain; CCA = Contribution of current assimilate; GY = Grain yield.

* and ** are significantly different at 5% and 1% levels of probability, respectively, using LSD.

LSD = Least significant difference.

under the D4 (milk to physiological stage) water deficit conditions compared to Suwan 4452. This result suggests that NK 40 has superior capacity for higher translocation of pre-anthesis assimilates during grain filling in moderate and severe water deficit environments.

In experiment I, the contribution of the current assimilates accumulated before and after anthesis to grain weight was substantially regulated by different levels of water deficit. The maximum contribution of current assimilates to grain weight was found under well watered conditions (D1) for all the genotypes, while the highest contribution of pre-anthesis assimilates to grain weight was observed for NK 40 under D4 (V17 to blister stage) water deficit conditions (Table 3). In experiment II, a higher CCA was recorded under water deficit at the V10 to anthesis

Table 3 Effect of water deficit and genotypes on translocation parameters of maize in experiment I at National Corn and Sorghum Research Center, Pak Chong, Nakhon Ratchasima, Thailand during 2010-11.

Treatment		SWD	SWDC	AT	ATE	CPAA	CCA	GY
Stage of water deficit	Genotype	(g per culm)	(%)	(g per plant)	(%)	(%)	(%)	($kg.ha^{-1}$)
Control	Pioneer 30B80	2.40^{k}	3.94^{n}	8.54^{h}	6.74^{i}	5.89^{i}	94.11^{a}	7732^{abc}
	NK 40	3.30^{j}	5.95^{m}	11.31^{g}	9.04^{gh}	7.21^{h}	92.79^{ab}	8371^{a}
	Suwan 4452	3.70^{i}	6.64^{l}	10.74^{gh}	7.61^{hi}	7.07^{hi}	92.93^{ab}	8094^{ab}
V10 to V13	Pioneer 30B80	3.21^{j}	6.67^{l}	10.61^{gh}	11.38^{f}	7.72^{h}	92.28^{b}	7329^{bcdef}
	NK 40	5.92^{gh}	13.15^{f}	24.63^{c}	24.06^{c}	17.05^{de}	82.95^{e}	7705^{abcd}
	Suwan 4452	3.48^{ij}	8.13^{j}	14.20^{f}	17.24^{de}	9.88^{g}	90.12^{c}	7663^{abcd}
V13 to V17	Pioneer 30B80	6.03^{g}	9.11^{i}	9.92^{gh}	11.44^{f}	11.64^{f}	88.36^{d}	6692^{ef}
	NK 40	8.46^{d}	17.63^{c}	28.16^{b}	23.35^{c}	20.76^{c}	79.24^{f}	7233^{bcdef}
	Suwan 4452	8.81^{c}	15.58^{e}	20.39^{d}	18.81^{d}	16.82^{de}	83.18^{e}	6464^{f}
V17 to blister	Pioneer 30B80	8.85^{c}	16.22^{d}	23.11^{c}	12.14^{f}	17.47^{de}	82.53^{e}	7055^{cdef}
	NK 40	15.34^{a}	24.29^{a}	36.55^{a}	29.30^{a}	26.51^{a}	73.49^{h}	7354^{bcde}
	Suwan 4452	6.89^{f}	11.08^{g}	17.02^{e}	17.96^{d}	17.74^{d}	82.26^{e}	7223^{bcdef}
Blister to PM	Pioneer 30B80	7.40^{e}	10.71^{h}	13.85^{f}	10.63^{fg}	10.81^{fg}	89.19^{cd}	6830^{def}
	NK 40	12.92^{b}	22.72^{b}	34.43^{a}	27.18^{b}	23.25^{b}	76.75^{g}	7897^{abc}
	Suwan 4452	5.63^{h}	7.14^{k}	14.85^{ef}	15.59^{e}	16.39^{e}	83.61^{e}	7888^{abc}
LSD (P = 0.05)		0.34	0.31	2.33	1.89	1.19	1.58	880.40

SWD = Stem weight depletion; SWDC = Stem weight depletion coefficient; AT = Assimilate translocation; ATE = Assimilate translocation efficiency; CPAA = Contribution of pre-anthesis assimilate to grain; CCA = Contribution of current assimilate; GY = Grain yield; PM = Physiological maturity.

D1 = Field capacity (control); D2, D3, D4 and D5 = Water deficit from V10 to V13 (42 to 56 d after planting), V13 to V17 (57 to 71 d after planting), V17 to blister (72 to 86 d after planting) and blister to physiological maturity, respectively;

* Mean values in the same column followed by different letters are significantly different at 5% level of probability using Duncan's multiple range test.

LSD = Least significant difference.

stage in both genotypes whereas water deficit in the milk to physiological stage produced a lower current assimilate contribution (Table 4). Severe water deficit inducing stomatal closing and limiting photosynthesis might have been the reason for the limited current assimilates contribution in the milk to physiological stage.

As shown in Table 3 in experiment I, the grain yield of maize varied significantly with the interaction effect of water deficit and genotype. The highest grain yield was attained by NK 40 under well watered management which was similar to Suwan 4452 under well watered (D1) conditions. In addition, NK 40 and Suwan 4452 produced similar grain yields under water deficit conditions, particularly when water was limited during the D5 (blister to physiological) stage and Pioneer 30B80 exhibited similar yields under well watered conditions. Under water shortage conditions, Pioneer 30B80 produced a lower maize grain yield.

In experiment II the grain yield of maize varied significantly due to the interaction effect of water deficit and genotype (Table 4). The highest grain yield was attained by NK 40 (7,436 kg.ha^{-1}) under the control conditions which was similar to yield for Suwan 4452 (6,741 kg.ha^{-1}) under control (D1) conditions. Under different water deficit conditions, NK 40 showed slightly higher grain yield than Suwan 4452. The lowest grain yield was produced by both genotypes when subjected to water deficit during the anthesis to milk stage.

Table 4 Effect of water deficit and genotypes on translocation traits of maize in experiment II at National Corn and Sorghum Research Center, Pak Chong, Nakhon Ratchasima, Thailand during 2011-12.

Treatment		SWD (g per culm)	SWDC (%)	AT (g per plant)	ATE (%)	CPAA (%)	CCA (%)	GY (kg.ha^{-1})
Stage of water deficit	Genotype							
Control	NK 40	41.67^{d}	18.47^{c}	29.68^{b}	13.15^{c}	27.65^{c}	72.35	7436^{a}
	Suwan 4452	12.33^{f}	6.62^{f}	7.75^{e}	4.16^{f}	7.97^{g}	92.03	6741^{ab}
V10 to anthesis	NK 40	11.67^{f}	8.36^{e}	12.96^{d}	9.28^{d}	15.17^{e}	84.83	5797^{cde}
	Suwan 4452	8.34^{f}	5.66^{g}	5.36^{f}	3.64^{f}	6.63^{g}	93.37	5637de
Anthesis to milk	NK 40	62.00^{b}	27.43^{b}	16.87^{c}	7.46^{e}	21.04^{d}	78.96	5608de
	Suwan 4452	21.00^{e}	11.23^{d}	8.08^{e}	4.32^{f}	10.85^{f}	89.15	5044^{e}
Milk to PM	NK 40	70.00^{a}	31.11^{a}	46.96^{a}	20.87^{a}	50.81^{a}	49.19	6456^{bc}
	Suwan 4452	53.00^{c}	28.19^{b}	30.92^{b}	16.45^{b}	35.70^{b}	64.30	6048^{bcd}
LSD (P = 0.05)		4.71	0.93	0.49	1.26	2.32	1.58	763.6

SWD = Stem weight depletion; SWDC = Stem weight depletion coefficient; AT = Assimilate translocation; ATE = Assimilate translocation efficiency; CPAA = Contribution of pre-anthesis assimilate to grain; CCA = Contribution of current assimilate; GY = Grain yield.

D1 = Field capacity (control); D2, D3 and D4 = Water deficit from: V10 to anthesis, anthesis to milk and milk to physiological maturity, respectively.

* Mean values in the same column followed by different letters are significantly different at 5% level of probability using Duncan's multiple range test.

LSD = Least significant difference.

CONCLUSION

The reduction in current photosynthetic assimilates during grain filling increased the contribution of the pre-anthesis assimilates reserved in the stems, which were translocated to the sink tissues (mainly grain) under the water deficit conditions. It is a physiologically complex process subjected to water stress during grain filling. Significantly higher assimilate translocation, assimilate translocation efficiency and contribution of pre-anthesis assimilates to the grain were achieved in the V17 to blister stage under the moderate water deficit and in the milk to physiological maturity stage under severe water deficit conditions, respectively, with the maximum stem dry weight depletion and stem dry weight depletion co-efficient. On the other hand, the highest contribution of current assimilates to maize grain was observed under the control conditions in experiment I and in under water deficit at the V10 to anthesis stage in experiment II, respectively. Under all experimental conditions, NK 40 always sustained a smaller reduction in grain weight. During grain filling, NK 40 exported 43.51 and 28.38% higher stem reserve dry matter compared to Pioneer 30B80 and Suwan 4452, respectively, under the moderate water deficit conditions and 46.20% higher stem reserve contribution compared to Suwan 4452 under the severe water deficit conditions. The strong source and sink and their balance in this genotype improved translocation and hence enhanced the contribution of pre-anthesis assimilates to grain during the grain filling period. Assimilate translocation showed significant positive relationships with stem dry weight depletion in both experiments I and II (R^2 = 0.81 and 0.87, respectively) and specific leaf weight depletion (R^2 = 0.93 and 0.88, respectively), whereas it showed a significant negative relationship with the source-sink ratio (R^2 = -0.53 and -0.84, respectively) and with the chlorophyll content (R^2 = -0.50 and -0.63, respectively).

ACKNOWLEDGEMENTS

The authors wish to acknowledge the Bangladesh Agricultural Research Council for financial support through a fellowship and also the Department of Agronomy, Kasetsart University, Thailand for providing the research facilities.

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