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Comparison of whole system of carbon and nitrogen accumulation between two maize hybrids differing in leaf senescence

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Abstract

A field experiment was conducted to investigate the carbon (C) and nitrogen (N) balance in relation to grain formation and leaf senescence in two different senescent types of maize (Zea *mays* L.), one stay-green (cv. P3845) and one earlier senescent (cv. Hokkou 55). In comparison with Hokkou 55, P3845 had a higher N concentration (N_c) in the leaves and a higher specific N absorption rate by roots (SAR_N), which indicated that a large amount of N was supplied to the leaves from the roots during maturation. This resulted in a higher photosynthetic rate, which supports saccharide distribution to roots. Thus, stay-green plants maintained a more balanced C and N metabolism between shoots and roots. Moreover, the coefficients of the relationship between the relative growth rate (RGR) and N_c, and between the photon-saturated photosynthetic rate (P_{sat}) and N_c were lower in P3845. The P_{sat} per unit N_c in leaves was lower in the stay-green cultivars, which indicated that high yield was attained by longer green area duration and not by a high P_{sat} per unit N_c in the leaf. Consequently, a high P_{sat} caused a high leaf senescence rate because C and N compounds will translocate actively from the leaves.

Additional key words: dry matter accumulation; photosynthetic rate; relative growth rate; specific N absorption rate by roots.

Introduction

Leaf senescence, as is quantified by leaf area duration (LAD), is a major determinant of yield in many crops (Patterson 1992, Thomas 1992, Osaki *et al.* 1993, Kumudini *et al.* 2002). Studies on 'stay-green' cultivars of several species confirm that delayed senescence increases the yield of determinate crops (Duvick 1992, Rajcan and Tollenaar 1999). Many senescence-related mutants have been found in crop plants that maintain leaf greenness after the grain-ripening stage, and these are referred to as stay-green or non-yellowing (Thomas and Smart 1993). Genotypes possessing the stay-green trait have a significant yield advantage compared with genotypes not possessing this trait, especially under postanthesis drought conditions (Borrell *et al.* 2000, He *et al.* 2001, 2002a,b, Kumudini *et al.* 2002).

Nitrogen from decomposed ribulose-1,5-bisphosphate carboxylase/oxygenase and chlorophyll is re-translocated to reproductive organs during the grain filling stage (Osaki *et al.* 1988a,b,c). For this reason, dry matter production is strongly regulated by N accumulation in plants (Osaki *et al.* 1992). It is important, therefore, to balance C and N metabolism for high yield production (Feller and Fisher 1994, Osaki *et al.* 1995a). The relative growth rate (RGR) is closely related to N_c in plants (Hirose *et al.* 1988, Pons *et al.* 1994, Wilkstrom and Agren 1995, Osaki and Shinano 2001). There is also a positive correlation between the leaf photon-saturated net photosynthetic rate (P_{sat}) and leaf N_c in various plants (Evans and Seemann 1989, Bondada and Oosterhuis 1998, Osaki and Shinano 2001) regardless of whether the variation in leaf N_c is due to the microenvironment, leaf age, or N availability (Reich and Schoettle 1988). Moreover, this relationship is stable across species or growth conditions (Field and Mooney 1986) when expressed per leaf mass (Reich *et al.* 1992). The coefficient of the RGR–N_c regression of the whole plant, or that of the P_{sat}–N_c regression of the individual leaves, may differ among species (Evans and Seemann 1989, Osaki and Shinano 2001). Therefore, the coefficient of RGR–N_c or that of P_{sat}–N_c within two maize cultivars with different senescent

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appearance may be different. The reasons for variation in the coefficient of RGR–N_c or that of P_{sat}–N_c related to grain formation and leaf senescence needs further study within two maize cultivars.

P_{sat} is regulated not only by N_c, but also by other factors such as leaf longevity. A negative relationship between P_{sat} and leaf longevity was confirmed (Field and Mooney 1986, Koike 1988, Reich *et al.* 1992, 1995, Wright and Cannon 2001), and the longevity of a leaf is intimately related to its N status (Thomas and Rogers 1990, Borrell and Hammer 2000, Borrell *et al.* 2000). Mass-based P_{sat} and leaf N levels are usually positively related to each other and negatively related to leaf thickness/density (low specific leaf area, SLA) and longevity (Reich *et al.* 1991, 1992, 1997, 1998, Haase *et al.* 2000, Craine and Reich 2001). Osaki and Shinano (2001) also found a negative correlation between P_{sat} and leaf longevity, and stated that the net C translocation rate (or photosynthetic rate) is closely related to the net translocation rate of N compounds from leaves. Therefore, leaf longevity decreases or increases when P_{sat} is high or low, respectively, because N is quickly or slowly translocated from leaves in correspondence to a high or low P_{sat}. Thus, a high photosynthetic rate results from a high translocation rate of C and N compounds from the leaves. In a canopy, new cultivars have improved towards increased leaf longevity, which means a longer LAD and relatively lower net assimilation rate (NAR). High yield is attained due to the high LAD and not to a high NAR (Osaki *et al.* 1991, 1993, Kumudini *et al.* 2002) since NAR is negatively correlated with LAD (Patterson 1992, Osaki *et al.* 1993).

Only a few reports are related to senescence of field-grown plants (Adams *et al.* 1990, Humbeck *et al.* 1996, Murchie *et al.* 2000, Lu *et al.* 2001, Osaki and Shinano 2001, He *et al.* 2002a,b). How this process is related to C and N translocation in two differently senescent types of maize remains unknown. To this end, a field experiment was carried out to investigate dry matter accumulation, RGR, N content, N accumulation, and SAR_N, to determine the relationship between C and N balance and grain formation in two maize hybrids differing in leaf senescence.

Materials and methods

Plants: Seeds of two hybrids of maize (Zea *mays* L.), the representative stay-green (cv. P3845) and the representative earlier senescent (cv. Hokkou 55), were soaked with water for germination. The germinated seeds were sown in the field of the Graduate School of Agriculture, Hokkaido University, Sapporo, Japan (43°03'N, 141°20'E) on 16 May 2001. Both the earlier senescent and stay-green hybrids are morphologically similar and do not differ in phenology. These two hybrid types have previously been used in studying physiological processes contributing to yield increase (He *et al.* 2001, 2002a,b). The plots (54 m^2) were arranged in a randomised complete block design with three replications and a plant density of 66 667 plants per ha (space: 0.60×0.25 m). Nitrogen [30 g m^{-2}, *i.e.* 300 kg(N) ha^{-1}; 50 kg N supplied by a rapid release fertiliser, and the other 250 kg N supplied as a slow release fertiliser], phosphorus [20 g(P_2O_5) m^{-2}], and potassium [20 g(K_2O) m^{-2}] were applied as basal applications with $(NH_4)_2SO_4$ or urea, superphosphate, and potassium sulfate, respectively.

Five to 10 plants in each replicate were sampled 42, 61, 82, 105, 124, and 134 d after sowing (DAS) from the vegetative growth stage to maturity. Samples were separated into leaf blades, stems, roots, and grains. For the dry mass and N_c determination, samples were dried at 80 °C for 72 h in an air-forced oven, weighed, and ground. Fifty plants were sampled at harvest to determine yield and yield components.

Determination of N_c, RGR, specific nitrogen absorption rate by root (SAR_N), and greenness: Nitrogen was determined by the Kjeldahl method (Hind 1993). RGR of the whole plant was calculated using the following equation: RGR = (1/M) (dM/dt), where M is the averaged total dry mass between two consecutive stages, dM is the difference of total dry mass [g m^{-2}] at the two stages, and dt is days (d) elapsed between the two stages.

Specific N absorption per unit dry mass of root [g(N) d^{-1} kg^{-1}(root dry mass)] was calculated according to Shinano *et al.* (1994) and Osaki *et al.* (1995b) using the equation: SAR_N = (1/M)(dN/dt), where M is dry mass of roots [g m^{-2}], N is the amount of nitrogen absorbed by the roots [mg m^{-2}], and t is the diurnal time [d].

Greenness was determined by the number of green leaves as a proportion of the maximum number of leaves, and a leaf was considered green if more than half of its area remained green (Birch 1998).

N_c and P_{sat} in individual leaves: P_{sat} was measured 54, 77, 96, 121, and 133 DAS in the field, and corresponding leaves were taken simultaneously for the measurement of N_c. To determine leaf position, individual leaves were marked from the ground level after emergence and P_{sat} was measured at photon saturation by placing the individual attached leaf in a transparent plastic chamber connected to an infrared gas analyser (model *ADC-3*, *Shimadzu*, Kyoto, Japan). A halogen lamp (*KTS-100R*, *Kenko Co.*, Tokyo, Japan) supplied irradiance of about 1 500 µmol m^{-2} s^{-1}. Air temperature, relative humidity, and the CO_2 concentration in the chamber were 20–25 °C, 40–50 %, and 350–370 g m^{-3}, respectively.

Statistical analysis: Standard analyses of variance were used to assess the significance of treatment means. Differences between treatment means were compared using the least significant difference (LSD). The regression was subjected to statistical analysis by *SPSS 10.0* (*SPSS for Windows 1999*).

Results

Yield and yield components: Both biomass and grain yield for the stay-green cv. P3845 were significantly higher than those for the earlier senescent Hokkou 55, and there was no significant difference in the harvest indexes between the two cultivars. Grain numbers per ear in P3845 were markedly higher than in Hokkou 55, although the 100-grain mass in P3845 was lower than in Hokkou 55 (Table 1).

Table 1. Yield and yield components in two maize hybrids. Means (±S.E.) of three replications. Significant differences at $p<0.05$ according to LSD test are marked with different letters.

Cultivar	100-grain mass [g]	Grain number per ear	Grain yield [g m^{-2}]	Biomass [g m^{-2}]	Harvest Index (HI)
Hokkou 55	32.70 ± 0.75a	438.8 ± 17.4 b	937.0 ± 22.2 b	2053.0 ± 36.8 b	0.456 ± 0.010 a
P3845	28.20 ± 0.64b	531.2 ± 15.5 a	1016.0 ± 21.8 a	2177.0 ± 70.0 a	0.467 ± 0.010 a

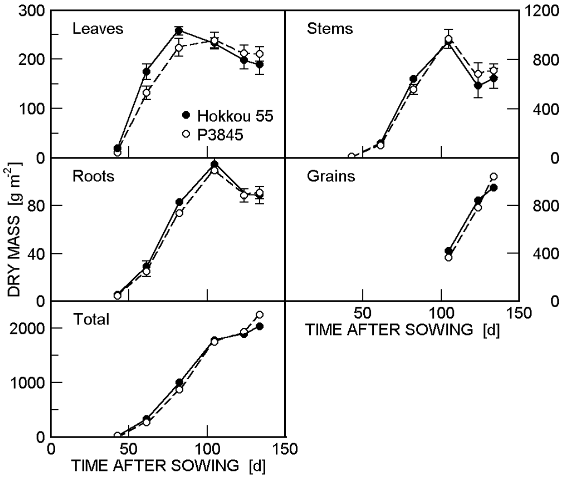

Fig. 1. Changes of dry matter accumulation in different parts of two maize hybrids. Means (±S.E.) with three replications.

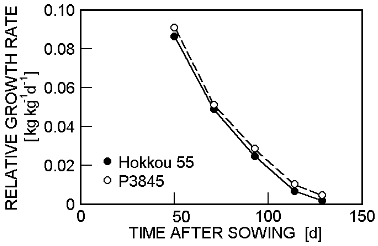

Fig. 2. Changes of relative growth rate in two maize hybrids.

Dry matter accumulation and RGR: There was a difference in the dry matter accumulation between the two hybrids. Total dry matter in P3845 was lower than in Hokkou 55 before flowering, but higher than Hokkou 55 after flowering until harvest (Fig. 1). For both hybrids, dry mass in the leaves and stems reached a maximum at 82 DAS (the time of flowering), and then declined with further growth. Leaf and stem dry masses in P3845 were lower than in Hokkou 55 before flowering and, following this, a higher dry mass was observed in the stay-green hybrid, P3845. Dry mass of grains in P3845 was lower than that in Hokkou 55 before the early maturation stage (124 DAS), but was higher than Hokkou 55 at harvest. The dry mass in roots in P3845 was slightly lower than in Hokkou 55 during the entire growth period. Osaki *et al.* (1995b) reported that root mass was not affected by N absorption or dry matter production, especially at the maturation stage, which means that root mass is not the only index of high yield.

The RGR declined with growth in both hybrids, and P3845 had a higher RGR through all growth stages compared with that in Hokkou 55 (Fig. 2).

N_c and N accumulation: Fig. 3 showed leaves, stems, and roots for both hybrids had the highest N_c at the early seedling stage, then N_c decreased with growth. The N_c in leaves, stems, and roots in P3845 was higher than in Hokkou 55 during the entire growth period. However, the N_c in the grain of P3845 was higher than in Hokkou 55 at 105 DAS, but decreased after 124 DAS until harvest. The lower N_c of grain in P3845 after 124 DAS was possibly caused by stronger dilution during grain filling, a result in accordance with previous reports (He *et al.* 2001, 2002a,b). The N accumulation in different organs followed trends similar to dry matter accumulation (Fig. 4).

SAR_N: The specific N absorption rate per unit dry mass of the root (SAR_N) was calculated to estimate the role of roots in N uptake (Shinano *et al.* 1994, Osaki *et al.* 1995b). The SAR_N in P3845 was higher than in Hokkou 55 during the entire growth period. This trend was in accordance with the RGR (Fig. 5). This result demonstrated that stay-green hybrid had a larger N absorption ability in roots during grain filling compared with the earlier senescent genotype.

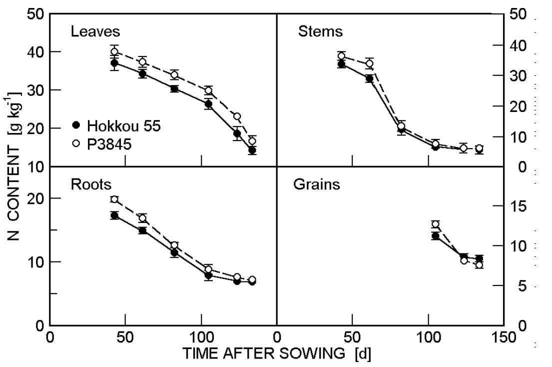

Fig. 3. Changes of nitrogen concentration in different parts of two maize hybrids.

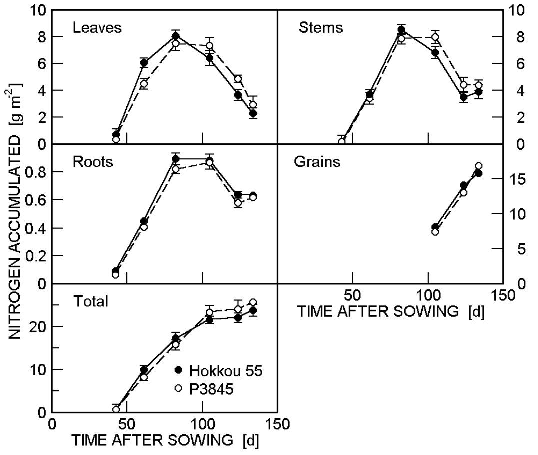

Fig. 4. The amount of nitrogen accumulated in different parts of two maize hybrids at successive stages.

Greenness is the standard used to quantify the percentage of green leaf area (Birch *et al.* 1998). Green area duration, or healthy area duration, was highly correlated with yield (Wolfe *et al.* 1988, Osaki *et al.* 1991, 1993, Kumudini *et al.* 2002). Fig. 6 shows the differences of greenness among the two cultivars after 75 DAS. As expected, there were fewer green leaves in Hokkou 55 than in P3845. At harvest, the green leaf area in P3845 was 51.1 % larger than in Hokkou 55, indicating that the stay-green hybrid delayed leaf senescence.

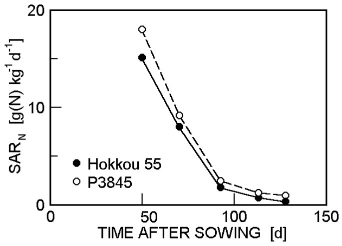

Fig. 5. Changes of SAR$_N$ in two maize hybrids.

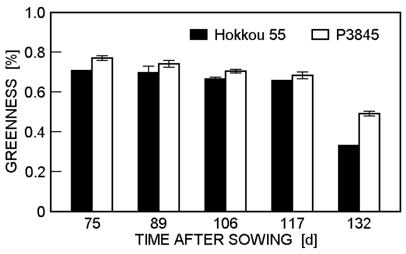

Fig. 6. Changes of greenness in two maize hybrids.

Discussion

There was a linear relationship between RGR and N$_c$ of the whole plant (Ingestad 1979, Hirose *et al.* 1988, Pons *et al.* 1994, Wilkstrom and Agren 1995). Furthermore, Osaki and Shinano (2001) found that RGR had a linear relation with N$_c$ of the canopy leaf, such that RGR = DMf Nc + RGR$_0$ (where DMf and RGR$_0$ are constants). They suggested DMf is different among cultivars and species and pointed out that C and N translocation was closely related and that leaf longevity was negatively related to the C and N translocation rate. In this research, RGR also displayed a linear relationship with N$_c$, such that RGR = DMf Nc + RGR$_0$.

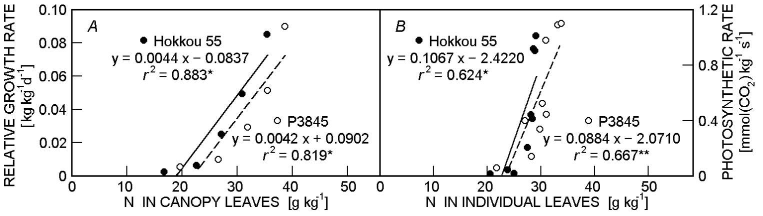

Fig. 7. Relationships between the RGR and N$_c$ in canopy leaves (*A*) and between the P_{sat} and N$_c$ of individual leaves (*B*) of Hokkou 55 (●, —) and P3845 (○, - - -). * and ** denote significance at the 0.05 and 0.01 probability levels, respectively.

The RGR–N$_c$ and P_{sat}–N$_c$ were estimated from the canopy and individual leaves, respectively. As the RGR indicated photosynthetic rate parameters, some relationship between RGR and P_{sat} is expected. When P_{sat} was calculated on leaf area basis, it was difficult to determine the RGR–P_{sat} relationship. Osaki and Shinano (2001) pointed out that P_{sat} could explain RGR across cultivars or species, when P_{sat} was expressed on leaf dry mass basis. Mass-based P_{sat} and leaf N contents are usually positively related to each other and negatively related to leaf longevity (Reich *et al.* 1991, 1992, 1997, 1998, Haase *et al.* 2000, Craine and Reich 2001). In our work, P_{sat} expressed on leaf dry mass basis was closely related with RGR. Osaki and Shinano (2001) noted that the C translocation rate per unit of N, from the entire or individual leaves, was highly correlated with the N translocation rate from lower leaves, and that both C and N translocation rates showed negative relationships with leaf longevity. In our study, DMf in Hokkou 55 was higher than that in P3845 (Fig. 7*A*). A higher DMf means higher net C translocation from the leaf canopy per unit of N_c. The net carbon translocation rate from leaves to grain in the earlier senescent hybrid was faster than that in the stay-green genotype, which accelerated leaf senescence. However, the rate of decrease of P_{sat} per unit of N_c in individual leaves was higher in Hokkou 55 (Fig. 7*B*). Therefore, both coefficients of the RGR–N_c (whole leaves) and P_{sat}–N_c (individual leaves) were lower in P3845 than in Hokkou 55, corresponding to slow senescence.

The correlation of RGR and SAR_N was similar to that of the RGR and N_c (Fig. 8), showing that RGR was high if SAR_N was high. In addition, the coefficient of the relation between RGR and SAR_N in Hokkou 55 was higher than in P3845.

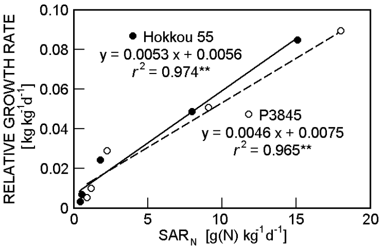

Fig. 8. The correlation between the RGR and SAR_N in the leaf canopy of Hokkou 55 (●, —) and P3845 (○, - - -). * and ** denote significance at the 0.05 and 0.01 probability levels, respectively.

To achieve high yield, N should be actively absorbed through roots during maturation (Osaki *et al.* 1991), and root activity should remain high during this period. Photosynthates, as energy substances, must be translocated to the roots to maintain high root activity. If a large amount of N is supplied to leaves from roots during maturation, photosynthesis in leaves will remain high, which supports the distribution of saccharides to roots. Thus, the growth of roots and shoots should mutually regulate each other.

In this study, N_c in leaves and SAR_N remained high during the maturation stage in P3845, indicating that stay-green hybrid supplied a larger amount of N to leaves from roots during maturation. This resulted in a higher photosynthetic rate, which in turn supported saccharide distribution to roots. Thus, the stay-green variety maintained a more balanced C and N metabolism between the shoots and roots. Earlier senescent hybrids had higher dry matter and N before flowering, but the higher C translocation rate per unit of N from the lower to upper leaves or apical organs accelerated the progress of leaf senescence. The lower N_c in leaves and the lower root SAR_N led to an imbalance of C-N between shoots and roots, which resulted in lower crop production.

Reich *et al.* (1997) mentioned that productivity of the individual plant increased with a decrease of leaf life span among species. We found that in maize a cultivar with a relatively longer leaf life span had a higher productivity at harvest. The difference in RGR was small before flowering, while RGR was higher in P3845 than in Hokkou 55 after flowering (Fig. 2). Although the difference was not large, it led to a higher yield. The strategy for achieving higher yields in maize may differ from the relationship observed in other species by Reich *et al.* (1997).

Higher productivity was attained with lower leaf activity per unit of nitrogen. Lower leaf activity was related to longer LAD. Thus, the strategies we elucidated that result in high productivity are: (*1*) a relatively low activity of leaf metabolism per unit nitrogen, and (*2*) maintenance of leaf longevity. Our results, and those of other authors, indicate that it is difficult to sustain both higher leaf activity and greater longevity.

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