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Effect of molasses on utilization of urea treated straw

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Abstract

Eight sheep of average live weight of 22.3kg were used in a completely randomized block design to study the effect of levels (0, 2, 4, 6 %) of molasses with urea treated straw (4 %) on dry matter intake (DMI), digestible crude protein (DCP), digestible dry matter intake (DDMI), digestible acid detergent fiber (DADF), rumen pH, rumen total volatile fatty acid (T-VFA), rumen ammonia (NH_3-N), blood urea nitrogen and nitrogen balance. Each of the four levels of supplementation were tested with 4 sheep. Daily DMI was calculated by recording the amount fed and the refusals. Rumen fluid was taken through a stomach tube and blood samples from jugular vein. Dry matter intake was increased by addition of molasses up to 4 % (from 534 to 638 g/d). Dry matter digestibility (DMD), organic matter digestibility (DOM), DCP and DADF were not affected significantly by the levels of molasses. Rumen pH showed a decreasing trend with increasing molasses levels. No significant change in the rumen NH_3-N was noted. The rumen T-VFA content increased by about 2 mmol/dl with 4 % molasses level compared to 3.9mmol/dl at no molasses addition. Hence, the molasses addition above 4 % increased the readily available energy. Blood urea nitrogen didn't vary and were found to be far below the fatal values reported. Hence, 4 % urea can safely be used to treat rice straw and be fed to sheep. Molasses addition at 4 and 6 % increased both the intake and faecal nitrogen. Retention of nitrogen increased up to 4 % molasses level and dropped at 6 % level. Hence, in view of the retention of nitrogen, 4 % molasses level is believed to be beneficial. It is concluded that addition of 2 % molasses is not suffcient to cause a beneficial change in any of the measured parameters. 4 % level cause considerable benefit.

Key words : Rice Straw, Urea Treatment, Molasses, Digestibility, Tropics.

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Introduction

A large portion of the world crop-by products are not used efficiently. Experiments are carried out to use rice straw, the major crop-by products in Asia, as a base feed for ruminants.

However, the low digestibility, low TDN and CP and the imbalance of minerals are identified to be the major constraints in the use of rice straw as a feed for ruminants. Physical, chemical, physicochemical or biological treatment are being adapted to enhance the feeding values of rice straw.

Urea-ammonia treatment of rice straw has been widely recognized as an effective mean to overcome the major deficiencies in the rice straw as a ruminant feed in tropical countries[10]. Urea-ammonia treatment of rice straw while giving physical effects, such as the degradation of the fibrous components, also provide non-protein nitrogen (NPN) to the ruminal microbes which in turn provides protein to the ruminants in the form of undegraded microbial proteins[15]. The water soluble carbohydrate content which is critically low in treated rice straw, reduces efficiency of organic matter digestion in the rumen[1, 5, 12, 14].

Supplementation of ingredients (such as rice bran) with high soluble carbohydrates has been demonstrated to increase the efficiency of the utilization of both untreated and treated rice straw in the rumen.

The objective of this study was to investigate the effect of levels of molasses as a source of soluble carbohydrate utilization of urea treated rice straw fed to sheep.

Materials and Methods

Place and Perid : This experiment was carried out at the University of Peradeniya, Peradeniya, Sri Lanka from October 24, 1990 to January 10, 1991.

Animal : Eight crossbred (Dorset Horn x Bikenary) sheep with an average body weight of 22.3kg were used at test animals.

Feed : Rice straw was used for this experiment. The rice straw was sun-dried for two days and stacked loosely.

Urea treatment : Standard method of urea treatment as recommended in Sri Lanka was used. Chopped straw (approx. 10cm) was thoroughly mixed with 4% (w/v) of urea in water at 1 : 1 ratio of straw : water (w/v). Treated straw was packed under air-tight condition in polyethylene bags and stored for 7 days before use[18]. Treatment was done until the 7th day before the end of the experiment.

Molasses supplementation : 0, 2, 4 and 6 % molasses (DM basis) was added to the straw just before feeding. Molasses, water solution was sprayed onto the straw using a hand sprayer, and mixed thoroughly. Feeding was done twice daily at 8 : 00 a.m. and 4 : 00 p.m. Feed was removed after 2 hr in both feedings.

Feeding : This experiment consists of 10-day adaptation period, followed by a 7-day preliminary period and 10-day total collection period. Animals were grouped according to their body weight. Randomized complete block design was used with 4 replications.

Data : Daily DMI was taken by recording daily feed offered and refusals. Rumen fluid was taken through a stomach tube for the analysis of rumen VFA, rumen NH_3-N and pH. Blood samples were taken from the jugular vein and analysed for blood urea nitrogen. During the total collection period, DMD, OMD and nitrogen balance was calculated.

Laboratory analysis : Feed and faecal samples collected daily were analysed for OM (draft oven), CP[2] and ADF[19]. Urea was analysed for nitrogen[2]. Rumen fluid samples were analysed for pH (electrometrically), NH_3-N[13] and T-VFA[13]. Blood plasma was used to determine blood urea nitrogen[6].

Statistical analysis : All data were statistically analysed by analysis of variance[3] and means were separated by Duncan's multiple range test[3]

Results and Discussion

Table 1. shows the DMI of the treatment groups. Except for the 2 % molasses diet, which showed a slight but non-significant decrease, all other levels of molasses supplementation increased the DMI. Kunju (1986)[11] reported a 103% increase in the DMI of straw in sheep by supplementation with urea-molasses lick block. However, on differences were observed in the DMI between 4 % and 6 % molasses groups. Hence, additions of molasses increase the intake. But this effect could be seen only up to 4 % level. The absence of an effect on intake at 6 % molasses over 4 % indicates addition of molasses at 4 % levels would be ideal to cause an increase in intake. Such difference in DMI in g/d were not significant when the refusals were converted into intake per kg body weight or intake per kg metabolic body weight. The values of DMI per kg body weight per day in this study is consistent with the reported range or intake for treated straw. However, on reported data are available to compare the absence of a change in DMI per kg body weight per day with various levels of molasses. Though not significant, the 2 % molasses caused a decrease in intake. This effect may partly be attributed to randomization of animals among treatment groups. The same animals in period I have fallen into the same group in period II. Such longer period of eating the same diet by these animals was not the case with the other animals. It may also be interpreted as a negative effect of molasses at as little as 2 % level, or intake or palatability.

Table 1. Intake of Urea Treated Straw.

	Level of Molasses in the Diet (% DM basis)				Level of Significance
	0	2	4	6	
DM Intake					
G/d	534^{ab}	486^{a}	638^{c}	635^{bc}	1 %
G/kg BW/d	24.4	21.6	25.2	27.1	N S
G/kg $BW^{0.75}$/d	52.5	47.1	56.4	59.6	N S

Means with dissimilar superscripts are significantly different.

Results of the chemical analysis of the diet is shown in Table 2.

Table 2. Chemical Composition of Urea Treated Straw

Component	Level of Molasses in the Diet (% DM basis)			
	0	2	4	6
DM	46.9	48.8	48.6	51.1
OM	89.4	89.7	89.8	89.1
CP	8.5	9.5	9.0	8.4
ADF	60.0	58.5	57.8	57.0
Cellulose	49.6	49.7	47.5	46.4

The digestibility of various molasses supplemented treatment groups are listed in Table 3. No significant changes in the DMD was observed in this trial between the molasses levels. However, the digestibility values are consistent with most reported data[4, 7, 17]. In this trial, at 4 % molasses level the digestibility of treated straw (4 %) is 45% while in a trial of Djajanegara (1986)[7], a value of 49% was observed with 1.5% urea treated straw, 42 g molasses and 33 g minerals. Higher values of DMD in Djajanegara's trial might have been caused by the addition of minerals. In another trial with cattle, Schieve et al. (1987)[17],

Table 3. Digestibility of Different Fraction of Urea Treated Straw

Component	Level of Molasses in the Diet (% DM basis)				Level of Significance
	0	2	4	6	
Digestibility (%)					
DM	44.2	43.0	45.2	45.5	NS
OM	52.9	52.3	53.0	53.1	NS
CP	47.3	50.0	49.1	47.1	NS
ADF	49.1	45.5	47.9	48.5	NS
Cellulose	49.5	46.4	47.5	48.6	NS

found no increase in the DMD on treated straw with supplementation of urea-molasses lick block. A significant increase in DMD% (+7.4%) by an addition of 400 g wet molasses was observed by Elliott (1986)[8]. No significant difference were caused by any of the molasses levels in the digestibility of any of the chemical components of the feed. Thus, the effect of addition of molasses up to 6 % levels is mostly increasing the intake and not changing the digestibility.

Table 4. Rumen Parameter and Blood Urea Nitrogen of Sheep Fed Urea Treated Straw.

Component	Level of Molasses in the Diet (% DM basis)				Level of Significance
	0	2	4	6	
Rumen pH	7.8^{b}	7.8^{b}	7.7^{ab}	7.5^{a}	5 %
Rumen NH_3-N (mg / dℓ)	12.6	17.0	13.1	18.1	NS
Rumen T-VFA (mmol / dℓ)	3.9^{a}	4.0^{a}	5.0^{a}	5.6^{b}	1 %
Blood Urea Nitrogen (mg / dℓ)	0.284	0.089	0.048	0.001	NS

Means with dissimilar superscripts are significantly different.

The rumen parameters like pH, rumen NH_3-N and rumen T-VFA, and the blood urea nitrogen are listed in Table 4. The average rumen pH of all the diet was 7.7. This pH value is surprisingly high. However, the high NH_3-N in the rumen could be attributed to this. As the pH could vary with time after feeding and the rate of change varies with type of feed[9, 11], it is difficult to draw a conclusion from the difference in pH. However, the pH slightly decreased when the level of molasses is increased 7.5 at 6 % molasses vs 7.8 at 2 % molasses. However, no significant changes in the rumen pH is seen up to the level of 4 % molasses addition. The rumen NH_3-N contents appear to be higher than normal reported values[11]. This might be responsible for the higher values of rumen pH in this study. Kunju (1986)[11] demonstrated an increase in the rumen NH_3-N after feeding, when compared to before feeding (195 vs 112 mg/ℓ) of rice straw and urea-molasses lick block. As Kunju in the same study reported greater changes in the NH_3-N contents throughout the hours of a day, with a single sample of rumen fluid taken after 4 hr after feeding, the NH_3-N values in this study are close to those of Kunju's post feeding values. The rumen T-VFA showed an increasing trend with increase in molasses level. Kunju (1986)[11] demonstrated an increase in the rumen VFA was concentrated by urea-molasses lick block. But significance in this increase is observed above 4 % molasses levels. This indicates an increase in readily available energy in the rumen with the addition of molasses. However, the soluble carbohydrate in the molasses was not found to help to increase the cellulose digestion as expected. No significant difference in the level of blood urea nitrogen was found. This suggests that addition of molasses up to 6 % did not cause any changes in the transfer of urea in the diet into microbial protein in the rumen. However, the decreasing trend in the blood urea nitrogen, with increasing levels of molasses gives an encouraging indication that some influence is there in the transfer of urea nitrogen of the diet into microbial protein. The blood urea nitrogen levels in this study are far below the fatal levels reported[16].

Results of the nitrogen balance analysis is listed in Table 5. Molasses addition at 4 and 6 % increased the intake and faecal excretion of nitrogen. However, significant increase in the excretion of urinary nitrogen occured only at 6 % molasses level.

Retention of nitrogen tended to incerease at up to 4 % molasses level and significantly dropped at 6 % level. This trend was also observed in nitrogen retention expressed as percent of intake and percent of absorbed. Addition of molasses at and above 4 % level increased both the nitrogen intake and excretion. Regarding the retention of nitrogen, 4 % molasses showed a very beneficial effect and above 4 % this effect was not found. In all the diets in this study, a positive nitrogen balance was observed. The reduction in the retained nitrogen is brought about by an increase in both faecal and urinary nitrogen losses. However, Gupta (1986)[9] observed a negative nitrogen balance with 5 % molasses and straw impregnated with 1 % urea. In the same study of Gupta, a positive nitrogen balance was observed when molasses level was raised to 10%.

Table 5. Nitrogen Balance of the Sheep Fed Urea Treated Straw.

Item	Level of Molasses in the Diet (% DM basis)				Level of Significance
	0	2	4	6	
Intake (g/d)	7.2^a	7.4^a	9.2^b	8.9^b	1 %
Excretion (g/d)					
Faecal	3.8^a	3.7^a	4.7^b	4.7^b	1 %
Urinary	1.1^b	1.0^{ab}	0.8^a	1.4^c	1 %
Total	4.9^a	4.6^a	5.4^b	6.1^c	1 %
Retention					
G/d	2.4^a	2.7^{ab}	3.8^c	2.9^{ab}	5 %
Percent of intake	31.7^a	36.7^{abc}	40.4^c	32.0^{ab}	5 %
Percent of absorbed	66.5^a	73.2^{abc}	82.0^c	68.0^{ab}	5 %

Means with dissimilar superscripts are significantly different.

Conclusion

It can be concluded that addition of molasses at 2％ level is not sufficient to cause a beneficial effect in the efficiency of use of urea-ammonia treated rice straw. At 6％ level very little increase in this efficiency was found. Hence, 4％ level of molasses would be an appropriate addition to cause a considerable benefit in the efficiency of urea-ammonia treated rice straw in sheep. It is also suspected that the effect of supplementation may vary between species and production levels of the animals. Positive effects of supplementation has been mostly reported with high producing animals, as production is confounded to intake and digestibility.

尿素処理稲わらの利用における糖蜜の効果

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摘　　要

尿素処理稲わらを反すう家畜の飼料として用いる際の糖蜜の添加効果を検討した。

尿素処理（4％）した稲わらに対して4水準（0，2，4，6％）の糖蜜を添加し，8頭の羊を用い，全2期の乱塊法で消化試験を行った。乾物摂取量は，糖蜜4％添加区で最も高い値（638ｇ／d）を示した。乾物，有機物，粗蛋白質，酸性デタージェント繊維，セルロース消化率には，各添加区間に有意な差が見られなかった。ルーメン内ｐＨは，添加水準の上昇に従って低下する傾向を示し，総ＶＦＡ濃度は逆に上昇した。これは，糖蜜がルーメン内微生物の栄養源として有効に利用されたことを示した。ルーメン内NH_3－Ｎは，糖蜜2％添加区と6％添加区において高い値を示したが，有意差はなかった。血中尿素態窒素濃度は，各添加区に低い値を示し，4％の尿素処理が家畜の生理上，安全に利用できることが確認された。窒素出納は，糖蜜4％添加区においても最も高い値（3.8ｇ／d，$p<0.05$）を示した。

以上の結果より，低水準の糖蜜添加において，4％添加が最も効果的であることが示唆された。

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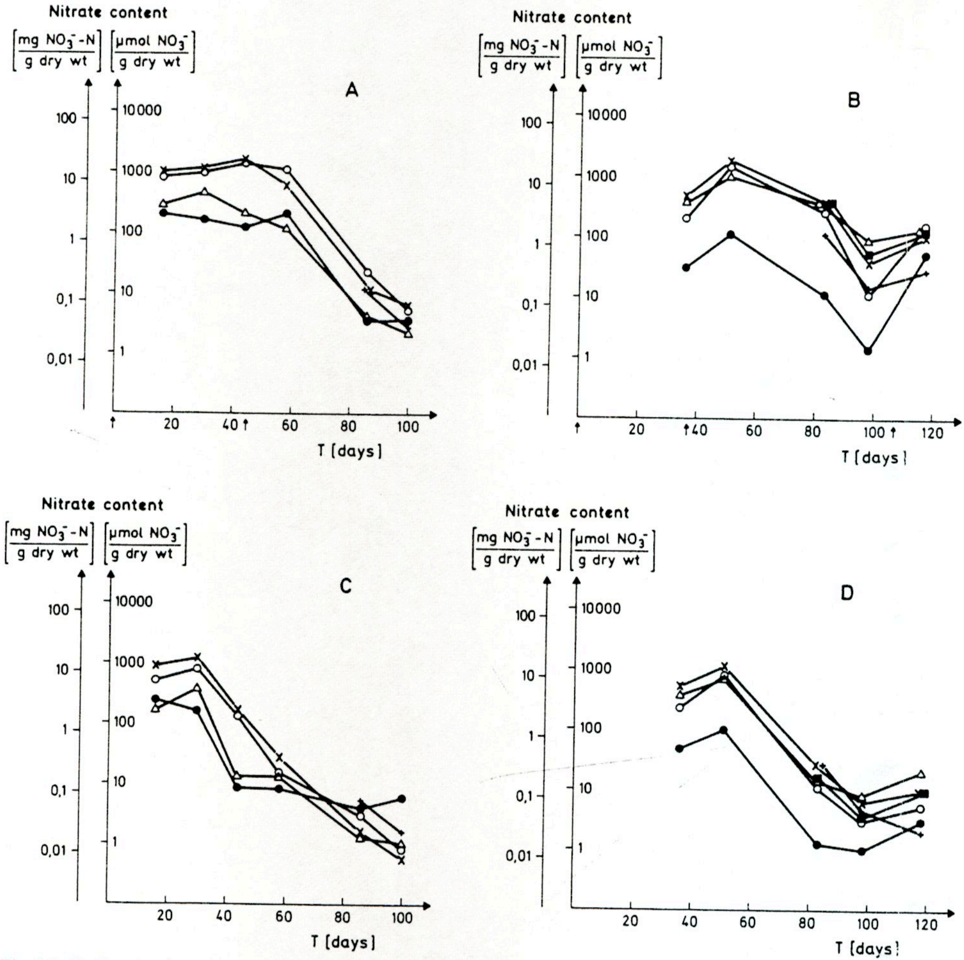

Fig. 9 A–D. Development of the nitrate content in different plant organs. **A** *Atriplex* high N set; **B** *Amaranthus* high N set; **C** *Atriplex* low N set; **D** *Amaranthus* low N set. ● laminae, ○ midribs + petioles (+ branches of the shoot axis, in the case of *Atriplex*), ■ branches of the shoot axis (in the case of *Amaranthus*), × shoot axis, △ roots, + reproductive organs, ↑ fertilization of the high N sets

whereas *Amaranthus* exhibited higher mean nitrate values in the roots.

Nitrate reductase activity

At the first and second samplings the young plants of *Atriplex* and *Amaranthus* evidenced high NRA values (*Atriplex* 11.5–15.7 µmol NO_2^-/g dry wt × h, *Amaranthus* 19.0–21.1 µmol NO_2^-/g dry wt × h), and the enzyme activities of the low N plants even exceeded those of the high N plants in some cases (Fig. 10). During this period the NRA of *Amaranthus* was on an average 28% higher than that of *Atriplex*. From the second to the third harvest a considerable decrease in NRA in both species was observed, and the NRA of high N and low N plants began to differ significantly (Fig. 10). During the following growth period the NRA per total plant showed continual slight decrease. At the end of the experiment minimal values of 0.7 µmol NO_2^-/g dry wt × h for both species were determined. The continually decreasing enzyme activity was negatively linearly correlated with the development of the dry weight in all series (Table 3). A significant correlation between NRA and the corresponding nitrate content of the plants, however, was only evident in the low N sets of both species (Table 3).

In both species the dominant proportion of the nitrate reduction took place in the leaves (Fig. 11). At the onset of flowering the reproductive organs – especially those of *Atriplex* – also exhibited considerable NRA. On the other hand, nitrate reduction in roots only played a minor role in all series, especially in plants of advanced age. The NRA of the shoot axis decreased drastically during plant growth and lignification. According to Pate's classification (1980), both species examined belong to the group of plants which reduce nitrate chiefly in the leaves. In young plants *Atriplex* had less NRA than *Amaranthus* in the laminae, but with

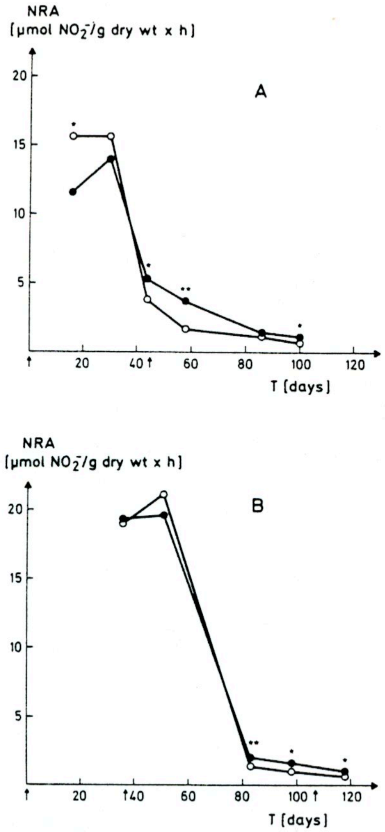

Fig. 10 A, B. Development of the NRA in the total plants. **A** *Atriplex*; **B** *Amaranthus*. ● high N set, ○ low N set, * $P<0.05$, ** $P<0.01$, ↑ fertilization of the high N sets

Table 3. Linear correlations between dry weight and NRA and nitrate content and NRA with *Atriplex hortensis* and *Amaranthus retroflexus* of various ages

Correlated parameters	Series	r	Slope	y-intercept	df	P<
Dry weight/ NRA	*Atriplex*					
	High N set	−0.9368	−0.339	11.98	4	0.01
	Low N set	−0.9431	−0.968	15.33	4	0.01
	Amaranthus					
	High N set	−0.9964	−0.331	19.80	3	0.001
	Low N set	−0.9938	−1.209	20.45	3	0.001
Nitrate content/ NRA	*Atriplex*					
	High N set	0.5144	0.010	2.79	4	n.s.
	Low N set	0.9991	0.038	0.96	4	0.001
	Amaranthus					
	High N set	0.6465	0.028	2.16	3	n.s.
	Low N set	0.9455	0.057	1.50	3	0.05

advancing age high N and low N *Atriplex* plants were able to maintain higher NRA in this important organ (Fig. 11). The late fertilization of *Amaranthus* resulted in only a slight increase of NRA in the laminae.

Transpiration

With the exception of the early morning (6^{00} and 8^{00} h) and the late evening hours (22^{00} h), substantially lower transpiration values were determined for the youngest fully developed leaves of the C_4 plant *Amaranthus* than for those of the C_3 plant *Atriplex* during the course of a day (Fig. 12). When the measurement at 22^{00} h is disregarded, no significant differences between the high N and the low N set of *Amaranthus* were observed. On the other hand the transpiration of the low N *Atriplex* was clearly and in most cases significantly higher than that of the corresponding high N plants. This result was verified in several repetitions (not illustrated).

The above results are confirmed by $\delta^{13}C$ data obtained from the high N and low N plants of both species. The average $\delta^{13}C$ values of the leaves in the high N and the low N set of the C_4 plant *Amaranthus* were exactly identical (−12.97‰; high N set s: 0.16; low N set s: 0.19). With *Atriplex* a C_3 plant-typical increased ^{13}C discrimination was observed, i.e. more negative $\delta^{13}C$ values, and furthermore a significant difference between the high N set ($\delta^{13}C =$ −28.01‰; s: 0.33) and the low N set ($\delta^{13}C =$ −28.95‰; s: 0.40) of the C_3 plant was evident. The more negative $\delta^{13}C$ value of the low N *Atriplex* indicates a more intense transpiration (i.e. reduced stomatal diffusion resistance and thus increased internal CO_2 concentrations) of the C_3 plant under low N conditions integrated over the growing season.

As indicated in Fig. 13, *Atriplex* leaves of various ages also usually reflected the distinct transpiration patterns of high N and low N plants. In both sets increasing transpiration values were observed to progress from the oldest (storey 1) up to the youngest fully developed leaves (storey 6). Not fully developed leaves (storeys 7 and 7 and 8, respectively), however, showed reduced transpiration rates. Whereas the mean radiation level available to the uppermost leaf storeys of the high N and low N plants was equal, the average radiation reaching the lower storeys decreased more pronouncedly with the high N plants, due to the denser leaf cover resulting intensified self-shading (Fig. 13). For the same reason the transpiration gradient from storey to storey was steeper with the high N plants than with the low N plants.

Discussion

As previously observed in competition experiments with the monocotylous C_3 plants *Hordeum vulgare* and *Avena sativa* and the C_4 plants *Panicum miliaceum* and *P. crus-galli* (Gebauer et al. 1987), the dicotylous C_3 plant *Atriplex hortensis* was also better able tolerate low N nutrition levels than was the C_4 plant *Amaranthus retroflexus* under our experimental conditions. This superiority of the C_3 plant in pure culture was enhanced under the competitive strain of mixed culture. During no phase of the plant growth period were any pronounced differences found respective of the organic N or the total N content in corresponding sets of the two species. The roots of the C_4 plant *Amaranthus* even tended to possess higher total N contents, a phe-

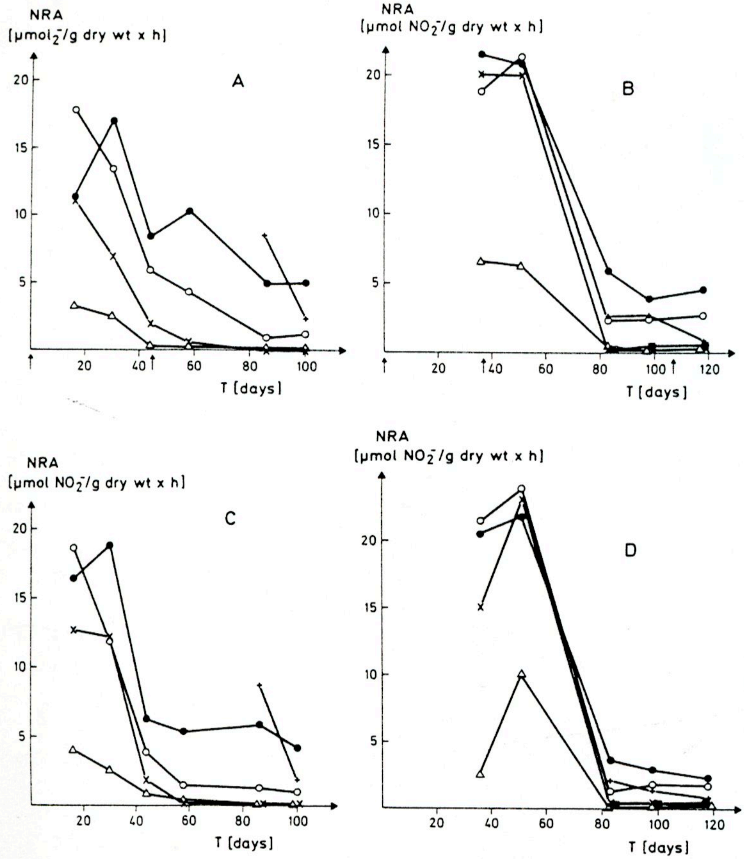

Fig. 11 A–D. Development of the NRA in different plant organs. **A** *Atriplex* high N set; **B** *Amaranthus* high N set; **C** *Atriplex* low N set; **D** *Amaranthus* low N set. ● laminae, o midribs + petioles (+ branches of the shoot axis in the case of *Atriplex*), ■ branches of the shoot axis (in the case of *Amaranthus*), × shoot axis, ▵ roots, + reproductive organs, ↑ fertilization of the high N sets

nomenon also observed by Öztürk et al. (1981). A dependence of the organic N content in plants on the nitrogen nutrition status and decreasing organic N concentrations during advancing plant age, as documented for *Atriplex* and *Amaranthus* in the present study, have also been described respectively of other species in similar orders of magnitude (Medina 1970; Janiesch 1973; Mooney et al. 1981; Rehder 1982; Field and Mooney 1983). Both the better tolerance of the C_3 plant of nitrogen starvation and the nearly identical organic N contents of the two species contradict the hypothesis of Brown (1978), according to which C_4 plants should have lower organic N contents and a competitive advantage under low N conditions due to their lesser investment in RuBP carboxylase. Thus once more the hitherto unresolved question arises as to the reason for the discrepancy between Brown's (1978) theoretical considerations and the results of our previous studies (cf. Gebauer et al. 1987). Schmitt and Edwards (1981) and Sugiyama et al. (1984) have forwarded the opinion that the comparatively low investment in the enzyme RuBP carboxylase of C_4 plants (10–35% of the soluble protein fraction in C_4 plants, but up to 50% in C_3 plants: Björkman et al. 1976; Ku et al. 1979; Sugiyama et al. 1984) might be compensated for by the characteristic investment of C_4 plants in the enzyme PEP carboxylase, which accounts for up to 15% of the soluble protein in these species (Hague and Sims 1980). Thus under comparable conditions and consideration of a species-specific degree of fluctuation, C_3 and C_4 plants might contain protein or nitrogen contents of the same order of magnitude. This argument might explain the nearly identical contents of organic N and total N observed in the case of *Atriplex* and *Amaranthus*, but not the competitive advantage of the C_3 plant under low N conditions.

The nitrate content and NRA of *Atriplex* and *Amaranthus* were comparable in magnitude to those described for other nitrophilous species (Austenfeld 1972; Janiesch 1973; Lee and Stewart 1978; Rehder 1982; Melzer et al. 1984). As could be shown here, however, the two species could be distinguished with respect to their nitrate distribution inasmuch as *Amaranthus* evidenced higher nitrate concentrations in the roots and *Atriplex* in the laminae. In addition, under conditions of marked nitrate starvation *Atriplex* – but not *Amaranthus* – was able to stabilize the nitrate content in the laminae at a low, but constant level. For this reason the C_3 plant maintained a higher activity of the substrate inducible enzyme nitrate reductase in the laminae under low N conditions. The better nitrate supply and the resulting higher NRA of *Atriplex* leaves under low N conditions may be related to the higher transpiration

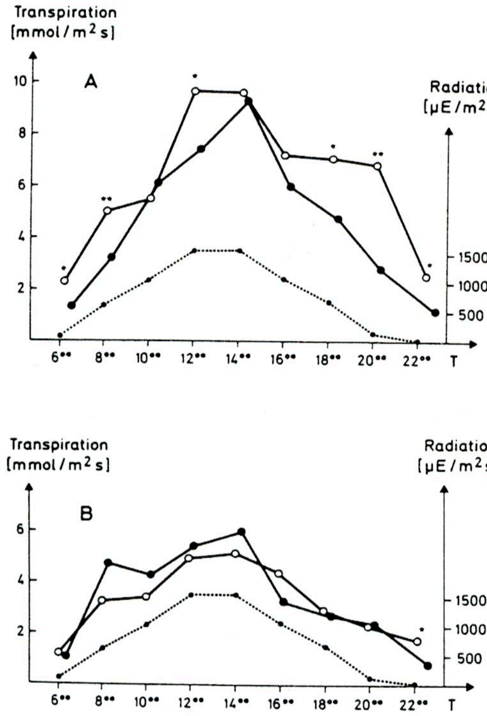

Fig. 12A, B. Transpiration of the leaves and photosynthetically active radiation during a day course at day 56. **A** *Atriplex*; **B** *Amaranthus*. ● high N set, o low N set, ··· radiation, * $P<0.05$, ** $P<0.01$

rates typical of C_3 plants (cf. review by Osmond et al. 1982) and as a consequence to an elevated xylem transport of nitrate from the source (i.e. the soil or the roots) to the sink (i.e. the leaves). The comparatively higher transpiration rate of the low N plants – only detected in the case of *Atriplex* – appears to represent a further adaptation to mineral starvation, with which the C_3 plant *Atriplex* is better equipped to deal than the C_4 plant *Amaranthus*, at least under conditions of sufficient water supply. A similar adaptation of the transpiration rate to the level of nitrogen supply has also been described by Schulze and Ehleringer (1984) for xylem-tapping mistletoes on nitrogen-fixing trees (with a high N content in the xylem sap) and non-nitrogen-fixing trees (with an essentially lower N content in the xylem sap). The lower transpiration rate of C_4 plants, regarded as a competitive advantage under low water conditions (Öztürk et al. 1981), is revealed to be detrimental to C_4 plants competing with C_3 plants under low N conditions when sufficient water is available. Further competition experiments incorporating C_3 and C_4 plants would be of great interest with respect to elucidation of the question as to which combination of the two factors N nutrition and water supply turns disadvantages into competitive advantages and vice versa. The comparatively low transpiration rate of C_4 plants also may lie at the root of the results of Christie and Detling (1982) and Edwards et al. (1985) to the effect that C_3 plants are indeed superior to C_4 plants under low N conditions and low temperatures, but are less competitive at high temperatures (see introduction). As transpiration responds to – among other things – temperature (cf. Osmond et al. 1982), the possibility cannot be excluded that only at comparatively high temperatures can C_4 plants attain transpiration rates sufficient to guarantee an optimum nitrate supply of the leaves, especially under low N conditions.

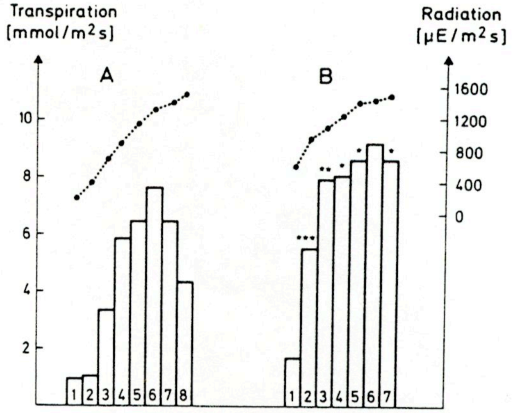

Fig. 13A, B. Transpiration and photosynthetically active radiation in different leaf storeys of the *Atriplex* high N set (**A**) and the *Atriplex* low N set (**B**) at day 57. Numbers *1–8* respectively *1–7* indicate the succession of the leaf storeys (*1* = lowest storey, *8* or *7*, respectively = uppermost storey). ··· radiation, * $P<0.05$, ** $P<0.01$, *** $P<0.001$

The shift of the shoot/root ratio in favour of the root proportion observed with *Atriplex* as well as with *Amaranthus* under low N conditions is interpreted by Davidson (1969) to represent an adaptation of the plants to mineral nutrient starvation. In our experiments the root length showed greater changes than did the root dry weight. This result indicates the tendency of low N plants to root the soil more intensively, and it may be that they partially counteracted the effects of nitrogen starvation by means of a greater root surface (cf. Robinson and Rorison 1983). The tendency to develop longer roots under low N conditions was more pronounced with *Atriplex* than with *Amaranthus*. Possibly this result is related to the different transpiration rates of the high N and the low N *Atriplex* plants. Further investigations are required, however, in order to thoroughly answer this question.

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