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The growth of *Bothriochloa pertusa* and *Dichanthium annulatum* in relation to crowding and herbage removal

R. S. Tripathi and G. P. Gupta

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The response of the two closely related sympatric fodder grasses, *Bothriochloa pertusa* (L.) A. Camus and *Dichanthium annulatum* (Forsk.) Stapf to increasing density and herbage removal has been compared. Both the species showed predominantly plastic reaction to density although at highest density (32 plants per pot of 25 cm diameter) some mortality, 9% in *D. annulatum* and 6% in *B. pertusa*, was also observed after 6 months growth. Increase in density from 1 to 32 plants per pot caused substantial decrease in production of tillers, leaves, aboveground herbage and total biomass of both the species. There was also some delay in flowering, and the percentage of fertile tillers was greatly reduced owing to increasing density. In the case of *D. annulatum*, a great reduction was noticed in the number and length of rhizomes and allocation of dry matter to them at higher densities. In general, the plastic reduction in various growth parameters due to crowding was comparatively greater in *D. annulatum*.

In both the grasses, the maximal yield was achieved when 4 plants per pot were grown. With an increase in density from 1 to 4, there was some increase in yield but this was never in proportion to increase in plant number per unit area. Any increase in density beyond 4 resulted in decreased yield per pot.

Both the grasses recovered well from the single treatment of clipping at 5 cm height which was done to simulate grazing. In terms of aboveground biomass production, *D. annulatum* seems to have suffered greater setback due to clipping than *B. pertusa*. The effect of crowding on the production of aboveground herbage appears to have been minimised due to clipping treatment.

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Сравнивали реакцию двух близкородственных видов кормовых трав *Bothriochloa pertusa* (L.) A. Camus и *Dichanthium annulatum* (Forsk.) Stapf. на увеличение плотности и удаление растительности. У обоих видов выявлена пластическая реакция на изменение плотности, хотя при самой высокой плотности (32 растения в горшке диаметром 25 см) установлена небольшая смертность – 9 % у *D. annulatum* и 6 % у *B. pertusa* через 6 мес. Увеличение плотности растений с 1 до 32 в 1 горшке вызывало существенное снижение продукции побегов листьев, надземных частей и общей биомассы у обоих видов. Наблюдалось также отставание в сроках цветения и процентном соотношении плодоносящих побегов, доля которых снижалась при повышении плотности. В случае *D. annulatum* наблюдалось сильное сокращение количества и длины ризомов и содержания сухого вещества при высокой плотности. В целом уменьшение разных параметров роста при загущении у *D. annulatum* оказывалось более сильным. У обоих видов трав максимальный урожай был при произрастании 4 растений в горшке. При повышении плотности с 1 до 4 наблюдалось некоторое увеличение урожая, но оно всегда непропорционально количеству растений на единицу площади. Повышение плотности растений свыше 4 приводило к снижению урожая в расчете на 1 горшок. Растения обоих видов хорошо справились после оной стрижки до 5 см высоты, которая проводилась для стимуляции роста. По показателям биомассы надземной продукции у *D. annulatum* задержка роста в результате стрижки была сильнее, чем у *B. pertusa*. Влияние загущения на продукцию надземных частей снижается в результате стрижки.

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1. Introduction

Bothriochloa pertusa and *Dichanthium annulatum* represent a sympatric pair of perennial grass species which occur quite commonly in the grasslands of several parts of India. Both are magnificent fodder grasses although *D. annulatum* has been reported to be more palatable, and is generally preferred (Whyte 1964). Both seem to be closely related as to habit, habitat, morphology and phenology. They can however, be distinguished on the basis of floral characters. The response of these two species to severity of intraspecific competition forms a part of our research programme on the interference between the closely related plant species. The examination of the reaction and growth modifications of each species in presence of the other under a variety of growth conditions (to be published later), of course, constitutes the main aspect of the programme. The study of the response of the species to crowding of its own individuals, is necessary before one attempts to analyse the more complex situation of interspecific competition. Further, the two grass species do occur in pure populations of varying densities in nature, and thus, the study of their response to increasing severity of intraspecific competition under controlled conditions may be related to field situations as well.

The two grasses are exposed to biotic influences of various kinds including grazing by cattle. The examination of their growth behaviour in areas with varying grazing stresses in field situation has revealed that with increase in grazing pressure, *D. annulatum* suffers a greater setback in its growth (Gupta 1977). Protection from grazing, according to Tiwari (1953–54) leads to better establishment of *D. annulatum* and *B. pertusa*. Grazing thus appears to be harmful for normal growth of these grasses and so, the influence of simulated grazing (by removing aboveground herbage through clipping) on the growth of these grasses was also included in the study.

2. Materials and methods

The seeds of the two grass species collected from the grassland on the Gorakhpur University Campus, between November, 1973 and March, 1974 were selected for uniformity and then were kept for germination in shallow trays filled with sandy soil under suitable temperature conditions. The seedlings were allowed to grow for 5 d in trays and then transplanted to earthen pots of 25 cm diam. and 30 cm depth filled with sandy loam soil (4 kg) and compost manure (1 kg) on 15 June, 1974. The pure populations of the two grasses were raised to give densities of 1, 4, 8, 16 and 32 plants per pot. The experimental design consisted of 2 species \times 5 densities \times 3 harvest times \times 3 replicates, thus involving ninety pots which were kept out of doors in the experimental garden, and were completely randomised. Each pot was

supplied with one litre tap water on alternate days. The first harvest (H_1) was taken on 15 August, 1974 after exactly 2 months of growth. Various growth variables e.g. number of tillers, leaf area per plant and above-ground, belowground and total biomass of the harvested plants were recorded to measure the response of the two grasses to density stress. For estimating biomass, the plant material was oven-dried at 80°C for 72 h. Mortality, if any, was also noted.

The plants of the remaining sixty pots were clipped at 5 cm height on 16 August, 1974. This was done to simulate herbage removal through grazing. The plants were kept under constant observation and their response to herbage removal and density stresses was noted after 2 and 4 months from the date of clipping i.e. after 4 and 6 months from the start of the experiment. The three harvests in time sequence have been abbreviated as H_1 , H_2 and H_3 and the densities used in the experiment have been presented as D_1 , D_4 , D_8 , D_{16} and D_{32} in the text.

3. Results

3.1. Plant and tiller mortality

No plant and tiller mortality was noticed up to 2 month growth at any densities but subsequently, at H_2 and H_3 some mortality occurred at high densities. At H_3 , there was 9% plant mortality in *D. annulatum* and 6% in *B. pertusa* at D_{32} . Percentage of dead tillers was not estimated but the tiller mortality was also higher in *D. annulatum* as was clear from the constant observation throughout the experimental period.

3.2. Production of tillers

Tiller production per plant was substantially reduced due to increase in density ($P < 0.001$) (Fig. 1). After 2 months growth, *D. annulatum* produced as many as 87 tillers per plant at D_1 while at high density (D_{32}) it produced only 8.4 tillers. Similar reduction in number of tillers produced per plant was also observed in *B. pertusa*. At the other two harvests the same trend was noticed.

The herbage removal does not appear to reduce the tillering capacity of the grasses as is evident from the larger number of tillers produced per plant at H_2 and H_3 . Tiller production per plant of *D. annulatum* was higher than that of *B. pertusa* at all densities and harvests (Fig. 1). Differences due to species were significant at 5% whilst the harvest times had no significant effect.

3.3. Effect on flowering

Flowering of both species was delayed due to increasing density. With increase in density per pot, there was conspicuous and significant decrease in percentage of

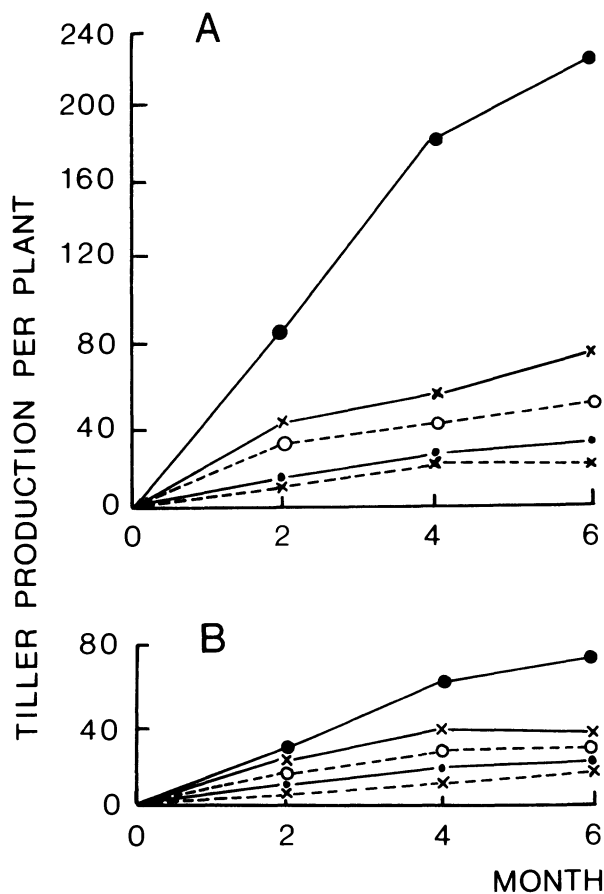


Fig. 1. Tiller production per plant of *Dichanthium annulatum* (Fig. 1A) and *Bothriochloa pertusa* (Fig. 1B) over 2, 4 and 6 months period in relation to increasing population density. Densities used are: 1 plant (●—●), 4 plants (x—x), 8 plants (o---o), 16 plants (-·-·-) and 32 plants (x----x) per pot.

spike bearing tillers in both the grasses ($P < 0.001$). The density stress affects the flowering potential of *D. annulatum* more adversely than that of *B. pertusa*, although flowering in *B. pertusa* was observed to take place 20–25 d earlier than in *D. annulatum*. Upto 2

months growth, however, there was no flowering under any density treatments (Tab. 1).

3.4. Leaf area per plant

Initially (at H_1), the leaf area per plant of *B. pertusa* was higher than *D. annulatum* at all the densities (Fig. 2) but at later harvest (H_2) which was taken after 2 months of clipping, *D. annulatum* produced greater leaf area. At H_3 , leaf area was not estimated primarily due to large proportion of dried leaves in both the species. The differences due to species and harvests were not significant while the density had significant effect even at 0.1% level.

3.5. Biomass production

Aboveground biomass

Aboveground biomass per plant of both the species showed substantial reduction ($P < 0.001$) with increase in degree of intraspecific competition (Tab. 2). *D. annulatum* at H_1 produced more aboveground biomass than *B. pertusa* at all the densities (species \times density

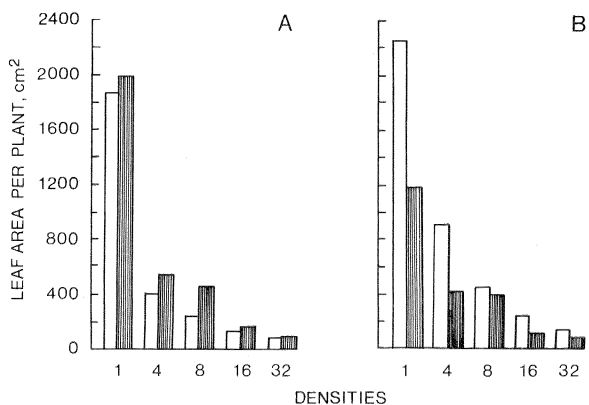


Fig. 2. Leaf area (cm^2) per plant of *Dichanthium annulatum* (Fig. 2A) and *Bothriochloa pertusa* (Fig. 2B) at H_1 (open columns) and H_2 (striped columns) as influenced by increasing density.

Tab. 1. The degree of flowering as indicated by the percentage of spike bearing tillers of *B. pertusa* and *D. annulatum* in relation to density.

Species	Harvests	Number of plants per pot				
		1	4	8	16	32
<i>B. pertusa</i>	H_1	No flowering				
	H_2	82.5	55.7	34.9	17.6	22.8
	H_3	61.1	45.2	31.7	29.2	15.5
<i>D. annulatum</i>	H_1	No flowering				
	H_2	18.0	19.2	5.5	2.1	1.0
	H_3	20.5	8.5	2.8	4.0	2.9

Tab. 2. Aboveground biomass (g) per plant and per pot (values given in parentheses) of *B. pertusa* and *D. annulatum* in relation to crowding.

Species	Harvests	Number of plants per pot				
		1	4	8	16	32
<i>B. pertusa</i>	H ₁	15.82 (15.82)	4.55 (18.20)	2.08 (16.64)	0.53 (8.48)	0.36 (11.52)
	H ₂	27.77 (27.77)	9.96 (39.84)	4.98 (39.84)	1.62 (25.92)	1.09 (34.88)
	H ₃	26.87 (26.87)	6.82 (27.28)	4.26 (34.08)	1.88 (30.08)	1.32 (42.24)
<i>D. annulatum</i>	H ₁	17.01 (17.01)	5.81 (23.24)	2.32 (18.56)	0.97 (15.52)	0.43 (13.76)
	H ₂	24.17 (24.17)	6.57 (26.28)	4.37 (34.56)	1.48 (23.68)	0.95 (30.40)
	H ₃	27.50 (27.50)	6.62 (26.48)	3.54 (28.32)	1.69 (27.04)	1.04 (33.28)

Tab. 3. Total biomass (g) per plant and per pot (values given in parentheses) of *B. pertusa* and *D. annulatum* at the three harvests as influenced by the increasing density.

Species	Harvests	Number of plants per pot				
		1	4	8	16	32
<i>B. pertusa</i>	H ₁	21.09 (21.09)	6.45 (25.80)	2.99 (23.92)	0.88 (14.08)	0.55 (17.60)
	H ₂	45.23 (45.23)	18.21 (72.84)	8.29 (66.32)	3.12 (49.92)	2.16 (69.12)
	H ₃	47.57 (47.57)	12.39 (49.56)	7.27 (58.16)	3.66 (58.56)	2.17 (69.44)
<i>D. annulatum</i>	H ₁	33.62 (33.62)	9.24 (36.98)	3.75 (30.00)	1.39 (22.24)	0.68 (21.76)
	H ₂	51.79 (51.79)	18.42 (73.68)	8.24 (65.92)	3.37 (53.92)	2.18 (69.76)
	H ₃	61.50 (61.50)	15.14 (60.56)	8.03 (64.22)	4.18 (66.88)	2.24 (72.96)

interaction significant at 5% level). *D. annulatum* seems to suffer greater setback after cutting as is evident from the relatively greater aboveground biomass of *B. pertusa* at H₂ and H₃ although the differences were not significant.

Aboveground biomass of the grasses per unit area showed some increase from D₁ to D₄ and D₈ but the increase in biomass was never commensurate with increase in density. At highest density, in fact, there was considerable reduction in the aboveground biomass of the plants of both the species harvested after two months growth (Tab. 2). Thus increase in density beyond a certain level, brings about reduction in aboveground herbage per unit area. The optimum density for achieving the maximal herbage yield seems to be 4 plants per pot in both the grasses if there is no herbage removal, e.g. at harvest 1. The effect of the high density appears to have been minimised due to cutting in both the grass species as indicated by the greater aboveground biomass values at higher densities

at H₂ and H₃ which were taken after 2 and 4 months from clipping.

Total biomass

Total biomass per plant of both the species was highly reduced ($P < 0.001$) with increasing density (Tab. 3, Fig. 3). At H₁, per plant total biomass production of *D. annulatum* was higher ($P < 0.05$) than that of *B. pertusa* at all the densities (Fig. 3). This trend was also observed at H₂ and H₃. After 6 months growth, total biomass values for *D. annulatum* at D₁ and D₃₂ were recorded as 61.5 and 2.2 g respectively whilst the corresponding values for *B. pertusa* were 47.6 and 2.2 g (Tab. 3). It appears that *B. pertusa* is less sensitive to density stress than *D. annulatum* as indicated by the degree of reduction in biomass from D₁ to D₃₂. Differences due to species were significant at 5%, due to harvest at 1% and due to density at 0.1% level and species × density interaction was significant at 5% level. The maximum total dry matter yield per unit area was recorded at D₄ in

Tab. 4. Total yield (g) per plant and per pot (including the clipped material from the first harvest) of *B. pertusa* and *D. annulatum* at varying densities during the experimental period.

Density per pot	<i>B. pertusa</i>		<i>D. annulatum</i>	
	Yield/plant	Yield/pot	Yield/plant	Yield/pot
1	68.7	68.7	95.1	95.1
4	24.7	98.8	27.7	110.8
8	11.3	90.4	12.0	96.0
16	4.5	72.0	5.6	89.6
32	2.7	86.4	2.9	92.8

Differences due to species are significant at 5% level and due to density at 0.1% level for per plant values. Differences due to species are significant at 5% level and due to density not significant for per pot values.

Tab. 5. Belowground biomass as percentage of the total biomass of *B. pertusa* and *D. annulatum* at the three harvests in relation to increasing density.

Species	Harvest	Number of plants per pot				
		1	4	8	16	32
<i>B. pertusa</i>	H ₁	24.9	29.3	30.5	39.7	34.0
	H ₂	38.6	45.3	39.9	47.9	49.3
	H ₃	43.5	44.9	41.3	48.7	38.8
<i>D. annulatum</i>	H ₁	49.3	37.1	38.1	30.4	37.0
	H ₂	53.3	64.3	46.9	56.1	56.2
	H ₃	55.2	56.2	55.8	59.6	54.6

both the grasses (Fig. 3). The data on total yield including the clipped material from the first harvest also confirmed the same trend (Tab. 4). The difference in total yield per pot of the two grasses at D₄ was, however, exaggerated with the inclusion of clipped material

in the yield data (compare Tabs 3 and 4). Statistically, the differences due to species were significant at 5% level while density had no significant effect on total yield per pot.

Belowground biomass

The contribution of underground parts to total biomass was far greater in case of *D. annulatum* as indicated by its higher percentage of belowground biomass (Tab. 5). Besides roots, some underground rhizomatous structures are also produced by *D. annulatum* which add to its belowground biomass. After cutting, *B. pertusa* showed a tendency to produce more aboveground biomass than *D. annulatum* although the differences were not significant. In terms of total biomass, however, *D. annulatum* is generally a better producer.

3.6. Rhizome production

Rhizomes were produced only in *D. annulatum* while *B. pertusa* did not produce any rhizomelike structure. At H₃ i.e. after 6 months from planting, a considerable quantity of rhizomes was produced by *D. annulatum*. The number, length and dry weight per pot of rhizomes as estimated at this harvest were found to be highest at D₄ and lowest at D₃₂ (Tab. 6). So, the rhizome production also showed plastic response to increasing degree of intraspecific competition.

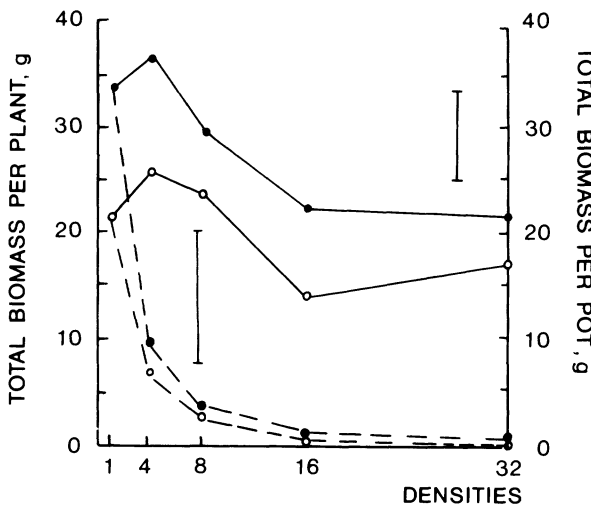


Fig. 3. Total biomass (g) per plant and per pot of *Bothriochloa pertusa* (per plant, ○ --- ○, per pot, ○ — ○) and *Dichanthium annulatum* (per plant, ● --- ●, per pot, ● — ●) after 2 months growth (without any herbage removal) in relation to population density. L.S.D. at 5% indicated in the figure.

Tab. 6. Rhizome number, total length and rhizome dry weight of *D. annulatum* per pot at H₃ as affected by the population density.

Character	No. of plants per pot					S.E. Means
	1	4	8	16	32	
Rhizome number per pot	25	31	30	24	16	±2.7
Total length of rhizome per pot (cm) ..	63.9	82.8	61.4	52.2	39.8	±7.1
Rhizome dry wt per pot (g)	2.67	3.60	3.28	2.30	1.33	±0.46

Tab. 7. Percentage reduction in tiller production, aboveground biomass and total biomass of *B. pertusa* and *D. annulatum* at H₃ and percentage reduction in leaf area of the grasses at H₂ with increasing population density.

	4	<i>B. pertusa</i> No. of plants per pot			4	<i>D. annulatum</i> No. of plants per pot		
		8	16	32		8	16	32
Tiller production	53	66	73	79	67	79	87	91
Leaf-area	66	66	91	94	74	78	92	96
Aboveground biomass	74	84	93	95	76	87	94	96
Total biomass	74	85	92	95	75	87	93	96

4. Discussion

Plant species generally exhibit two types of reactions to increasing density: (1) increased mortality and (2) greater plastic reduction in size and reproduction potential. Some plant species show greater plastic reaction e.g. *Agrostemma githago* (Harper and Gajic 1961) and *Capsella bursa pastoris* (Palmlblad 1968a) while others like *Papaver* species (Harper and McNaughton 1962) and *Plantago major* (Palmlblad 1968a) respond to increasing density predominantly through mortality. In the present study, *D. annulatum* showed greater mortality and plasticity than *B. pertusa*. The plastic reduction in various growth characters of the two grass species due to increasing density has been compared in Tab. 7.

The percentage reduction in all the variables recorded was higher in *D. annulatum* than in *B. pertusa* (Tab. 7). The plastic reduction in growth characters of both the grass species seems to be highly correlated with increasing density i.e. with severity of intraspecific competition. The reduction in dry matter yield and other growth variables caused due to density increase has been reported by many workers (Koyama and Kira 1956, Yoda et al. 1963, Tripathi 1968, Palmlblad 1968b, White and Harper 1970). Recently, Bazzaz and Harper (1976) have established a negative correlation between mean plant weight and number of surviving individuals in mixed populations of *Sinapsis alba* and *Lepidium sativum*.

From the viewpoint of regulation and growth of population the reduction caused in reproduction potential seems to be of more vital significance. A very great reduction, 91% in *D. annulatum* and 79% in *B. pertusa*, has been observed in production of tillers which are considered as important units of propagation in grasses.

Not only the flowering and fruiting were delayed due to increase in density, also there was sufficient reduction in percentage of tillers that bore spikes (Tab. 1). At H₃, percentage of spike bearing tillers of *D. annulatum* was reduced from 20.5 at D₁ to 2.9 at D₃₂, the corresponding values for *B. pertusa* being 61.1 and 15.5%. Obviously, the seed production in the two grasses will also be adversely affected which in turn may curtail the future growth of the population. Unfortunately, the valuable information on seed production could not be collected because most of the seeds were readily shed and by the time of H₃, they all vanished from the parent plants. However, on the basis of reduction in flowering it could be argued that the seed production would be drastically reduced on account of increase in density. The delay in flowering due to increased density has also been recorded in *Coryza canadensis*, *Plantago major* and *Senecio viscosus* (Palmlblad 1968a), and in tall fescue (Harkess 1970). Palmlblad (1968b) further observed that the seed production per individual of *Senecio sylvaticus* and *S. viscosus* increased with the intensity of reduced competition.

Of the two grasses, *D. annulatum* produces some rhizomatous structures that turn upward to be subsequently converted into tillers. The number of rhizomes per pot, their total length and dry weight were very much reduced at high density (Tab. 6). If considered on per plant basis, the increased density stress on reproductive potential can be much more pronounced. Thus, the increased density may regulate the population size of the two grasses by reduced seed output and decreased potential of vegetative reproduction as indicated by the reduced tiller production in both the species (Fig. 1) and reduction in rhizome production of *D. annulatum* (Tab. 6). Such a plastic reduction in re-

productive capacity at high density has also been reported in *Agrostemma githago* (Harper and Gajic 1961). The crowding of johnsongrass *Sorghum halepense* plants has recently been shown by Williams and Ingber (1977) to delay the formation of rhizomes, tillers and panicles and to cause reduction in dry weight accumulation in its reproductive structures.

The aboveground biomass of *B. pertusa* was found to be higher at the harvests taken after clipping whilst at H_1 when there was no clipping, *D. annulatum* produced more aboveground herbage than *B. pertusa*. This shows that *D. annulatum* is more susceptible to herbage removal than *B. pertusa*. Yield per unit area of both the grass species at D_4 registered an increase over the yield at D_1 but the magnitude of increase was never in proportion to the increase in number of individuals per unit area (Fig. 3). The maximum yield was achieved at D_4 (4 plants per pot) when the grasses grew for 2 months without any herbage removal. An increase in density beyond 4 plants per pot brings about reduction in yield per unit area. This information may be exploited while undertaking the cultivation of these grasses for fodder. According to Harper and Gajic (1961) the plastic reaction of individual plants to increasing density may exactly compensate or even over-compensate for increasing number of plants per unit area to give a constant final yield curve or parabolic curve. The yield per unit area has been reported by many workers to be either levelled off or reduced at high densities as in case of *Helianthus annuus* Clements et al. 1929) and *Vicia faba* (Hodgson and Blackman 1956, 1957). Similarly, the two grasses under study also show reduction in final yield per pot at high densities especially when they are left to grow undisturbed at H_1 (Fig. 3).

In absence of competition, it could be assumed or expected that at high density, say at D_{32} , the grasses will give 32 times as much yield as found at D_1 but this does not happen because of the limiting resources and increasing demand by the greater number of individuals at high density. Thus, the expected values of biomass production of both the grasses per unit area would be much greater than the actual observed values at high density (Fig. 4). The differences in expected and observed values as indicated by their ratios, were exaggerated with increasing density in both *D. annulatum* and *B. pertusa* at all the three harvests. The ratios between the expected and observed values were generally higher in *D. annulatum* than *B. pertusa*, which again indicates the greater plastic response of *D. annulatum* to increasing density.

The increased degree of intra-specific competition causes strong plastic reaction in both the grasses so much so that their reproductive potential is greatly reduced. It may be noted that "the reactions to increasing density" according to Harper and Gajic (1961), "confer on population the properties of self-regulating systems by permitting a rapid increase in numbers from low densities but placing self-curbing restrictions on further

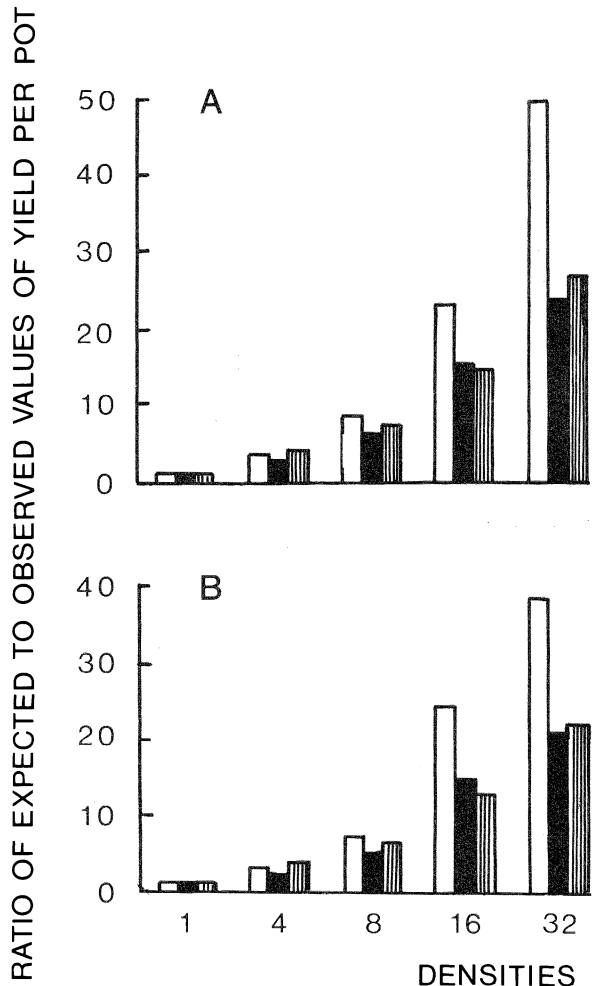


Fig. 4. Ratios of expected to observed values of the total biomass per pot of the two grasses at the two harvests. Fig. 4A - *Dichanthium annulatum* and Fig. 4B - *Bothriochloa pertusa*. (open columns for H_1 ; closed columns for H_2 and striped columns for H_3).

expansion as the density becomes greater". This seems to be largely true with *D. annulatum* and *B. pertusa* in view of the marked decrease in their growth and reproductive potential at high densities.

Both the grass species recovered well from the clipping treatment which was done to simulate grazing. *D. annulatum*, however, appears to be more susceptible to herbage removal than *B. pertusa* as indicated by the lesser aboveground biomass of *D. annulatum* at H_2 and H_3 that were taken after 2 and 4 months from clipping. Single clipping treatment after 2 months growth seems to have minimised the effect of density on the aboveground biomass production. In field situations, however, these grasses are grazed much more frequently and it would indeed be very interesting if the behaviour of the two grasses is studied in relation to frequent herbage removal spread over different stages of their growth cycle.

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