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ECOPHYSIOLOGICAL ANALYSIS OF GROWTH AND YIELD POTENTIAL OF RICE UNDER DRYLAND CONDITIONS

Analyse écophysiologique de la croissance et du rendement du riz en milieu terrestre

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RESUME

Six variétés de riz indica ont été cultivées en milieu terrestre avec approvisionnement d'eau résultant uniquement des précipitations. Des différences significatives de biomasse ont été observées au niveau variétal. Le taux relatif de croissance (RGR) montre une corrélation positive significative avec le taux net d'assimilation (NAR). La productivité primaire nette est étroitement associée à l'index de surface foliaire (LAI) et à l'index de chlorophylle (CI), toutefois sa grandeur est en liaison avec le taux net d'assimilation. Une corrélation positive significative a encore été observée entre la teneur relative en chlorophylle de l'épi à l'époque de l'épiage et le rapport pondéral épi/plante. Une bonne croissance antérieure à l'épiage, comme c'est le cas pour la variété Saket 3, semble tamponner l'effet d'une sécheresse ultérieure. Les variétés capables de remobiliser les réserves organiques accumulées avant le développement de l'épi pour la production des caryopses, et également capables de recouvrer un taux d'assimilation net positif pendant le stade de remplissage des graines,présentent un rendement potentiel économique meilleur.

ABSTRACT

A time series analysis of structural and functional growth attributes of six varieties of indica rice made under droughted rain-fed conditions revealed varietal variation in growth pattern and yield potential. A significant varietal variation occurred in biomass accumulation with age. The relative growth rate (RGR) exhibited a positively significant correlation with net assimilation rate (NAR). Net

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primary productivity was closely associated with leaf area index (LAI) and chlorophyll index (CI); however, its magnitude was accertained in combination with NAR. A significant positive correlation occurred between relative chlorophyll content in the ear at grain-filling time and ear to plant weight ratio. A good pre-heading growth, as in Saket 3, seems to buffer the effect of post-earing drought. The varieties capable of remobilizing pre-heading organic reserve to the grains substantially, and also capable of recovering NAR during grain-filling stage showed better economic yield potential.

INTRODUCTION

In recent years efforts have been made in India to increase paddy production by extending its acreage to abandoned rain-fed upland areas. However, as the rice plants are morphologically, anatomically, and physiologically adapted to submerged soil conditions, their ecological adjustment on upland soil is a major problem. The soil and atmospheric environments of paddy ecosystems under inundated and dryland cultural conditions are very different (IRRI, 1975). The most severe danger to rain-fed rice is the constant threat of drought causing moisture and heat stress to the plant, thereby affecting the growth and yield. To overcome this problem, drought resistant varieties of low-water-demand are being improved and tried. However, less attention has been paid to understanding the influence of growth pattern on yield potential of the improved varieties. Information on the variation in structure and function of leaf canopy and nonfoliar assimilatory parts, dry matter production efficiency with age, and on the final partitioning of dry matter as economic yield is required to understand the yielding strategy of a variety under natural drought conditions. With this approach, a time series analysis of the growth pattern of six *indica* rice varieties was made under rain-fed upland conditions and the findings have been discussed in this paper to elucidate varietal variation in yield potential.

MATERIALS AND METHODS

The investigation was carried out on six high yielding *indica* rice varieties, viz., Saket 3, Cauvery, Pusa 2-21, Ratna, CR 44-1 and Jaya which were on trial at the Dryland Agriculture Farm, Banaras Hindu University, Varanasi (23° 18' N and 81° 01' E). The seeds at the rate of 100 kg Ha^{-1} were sown in 5 cm deep and 30 cm apart drills in triplicate randomised plots (5 x 3 m) on well-drained upland soil. Fertilizers at the rate of 66, 50 and 50 kg ha^{-1} for N, P and K, respectively, were applied as basal manuring at sowing. Again, 33 kg ha^{-1} N was topdressed at pre-heading stage. The crops were totally dependent on rainfall. Handweeding was carried out whenever necessary.

Every fortnight, commencing from the 16th day after sowing till ripening, 10 - 15 plants along with the monoliths (15 x 15 x 30 cm) were sampled from each replicate plot to estimate their leaf area, dry weight and chlorophyll content. After carefully washing off the soil adhering the roots, the component plant parts were separated and their dry weights were recorded after drying the samples at 80° C to a constant weight. Standing dead parts, visible from the third harvest onward, were also sampled, dried, weighed and added for total weights to the respective compartments.

Leaf area was measured by determining total dry weight of leaves on a plant, and leaf area to leaf dry weight ratio of subsamples at each harvest. Chlorophyll content in different green parts (stem including leaf-sheath, lamina and ear) was estimated according to ARNON (1949), and converted on dry weight basis.

Growth indices such as net primary productivity (NPP), relative growth rate (RGR), net assimilation rate (NAR), chlorophyll content ratio (CCR), leaf area index (LAI), and chlorophyll index (CI) were calculated as under :

$$\text{NPP } (g\ m^{-2}\ d^{-1}) = \frac{W_2 - W_1}{t_2 - t_1}$$

$$\text{RGR } (g\ g^{-1}\ d^{-1}) = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}$$

$$\text{NAR } (g\ mg^{-1}\ Chl\ d^{-1}) = \frac{(W_2 - W_1)\ (\ln Chl_2 - \ln Chl_1)}{(Chl_2 - Chl_1)\ (t_2 - t_1)}$$

$$\text{CCR } (mg\ Chl\ g\ d\ wt.) = \frac{(Chl_2 - Chl_1)\ (\ln W_2 - \ln W_1)}{(W_2 - W_1)\ (\ln Chl_2 - \ln Chl_1)}$$

Where W_1 and W_2 are the dry weights and Chl_1 and Chl_2 are chlorophyll contents at times t_1 and t_2, respectively.

$$\text{LAI} = \frac{\text{leaf area}}{\text{ground area}}$$

$$CI = \frac{\text{Total chlorophyll content}}{\text{ground area}}$$

In the formula for NAR, conventional use of leaf area has been replaced by chlorophyll content (MISRA & SINGH, 1975), and CCR has been calculated in place of leaf area ratio (LAR).

To compute per cent of pre-heading reserve allocated to the ear, the final biomass was partitioned into pre-heading and post-heading net assimilates. Pre-heading reserve was calculated as under :

$$\text{Pre-heading net assimilate } (g\ m^{-2}) = \text{Biomass at harvest prior heading} + \text{Productivity } (g\ m^{-2}\ d^{-1}) \times (\text{Age at heading} - \text{Age at harvest prior heading})$$

The dry weight in excess of the post-heading biomass in the ear was considered to have come from the pre-heading reserve and was calculated as :

$$\text{Per cent of pre-heading reserve allocated to ear} = \frac{\text{Ear d wt. - Post-heading net assimilate}}{\text{Pre-heading net assimilate}} \times 100$$

ENVIRONMENTAL CONDITIONS DURING CROP SEASON

The environmental conditions prevailing during the crop season are indicated in table I. The total rainfall received during the experimental year, 1972, was 731 mm as against the expected long term average of 1100 mm, while during crop life it was only 423 mm as against the long term average of 990 mm for the corresponding period of the previous years. The rainfall during the post-earing phase, in particular, was very scanty amounting to 17 % of the total during the crop life. Inundation of the field prevailed for 4 days at the most, between 44 and 47 days after sowing while the crop was in the vegetative phase. Of the several drought spells the crop grew through, two were very pronounced : one during the seedling stage, between 8 and 25 days after sowing, and the other during the post-earing phase, from the 89th day onward till maturity. During these spells soil moisture fell as low as 8 %, which was much below the field capacity (17 %), inducing wilting. Thus on the whole, the environmental conditions prevailing during the lifetime of crop were of an arid nature, in the context of rice cultivation.

Month	Rainfall (mm)	Temperature (°C)		Relative humidity (%)	
		maximum	minimum	maximum	minimum
July	170.5	35.0	27.5	74.7	65.3
August	159.4	32.9	25.6	86.9	71.3
September	69.9	32.8	24.4	85.9	66.8
October	32.5	32.1	19.7	79.0	53.8
November	nil	30.9	13.9	77.7	40.4

Tab. I : Environmental conditions at Banaras Hindu University Campus, Varanasi during crop season (9 July to 17 November 1972).

RESULTS

Biomass.

Dry matter production increased progressively with age, except for a decline at 78 days in Saket 3 and at the final harvest in Pusa 2-21, Ratna and CR 44-1 (Tab. II). Biomass differed significantly among the varieties. Maximum biomass at the final harvest was produced by Cauvery, followed by Jawa, Saket 3, Ratna, Pusa 2-21 and CR 44-1 in the decreasing order.

Productivity.

A time course trend of productivity is depicted in figure 1. Analysis of variance for varietal variation in the rate of dry matter production was not significant. The rate, however, differed significantly with age (LSD = 10.33, df = 6, P = 0.05). The age at which maximum productivity was achieved, varied with the variety. It occurred during the grand period of vegetative growth (63 days) in Saket 3, with newly emerged ears at 78 days in Ratna and during the late post-earing phase in Pusa 2-21, Cauvery, CR 44-1 and Jawa. Maximum productivity was recorded by Saket 3, followed by Cauvery, Ratna, Jaya, Pusa 2-21 and CR 44-1. Productivity was closely associated with LAI and CI with an exception at 63 days in Cauvery, Ratna and CR 44-1 (Fig. 1).

Variety	Age (days)						
	16	31	46	63	78	93	Final*
Saket 3	8.25	38.77	118.14	663.00	589.44	706.02	934.79
Cauvery	18.79	64.16	260.10	466.74	697.94	1164.96	1224.49
Pusa 2-21	12.89	44.57	144.10	423.16	575.13	836.29	671.61
Ratna	14.46	38.08	147.49	228.47	625.15	978.94	887.60
CR 44-1	15.46	38.09	142.42	251.53	459.82	710.61	405.62
Jawa	9.23	39.61	119.43	246.12	366.66	430.38	1091.75

Tab. II : Varietal and age variations in biomass (g m^{-2}) of six rice varieties grown under rain-fed upland conditions. LSD for variety = 137.27, P = 0.05 : LSD for age = 200.57, P = 0.01. *Saket 3 : 104, Cauvery : 101, Pusa 2-21 : 110, Ratna : 112, CR 44-1 : 116, Jaya : 127 days.

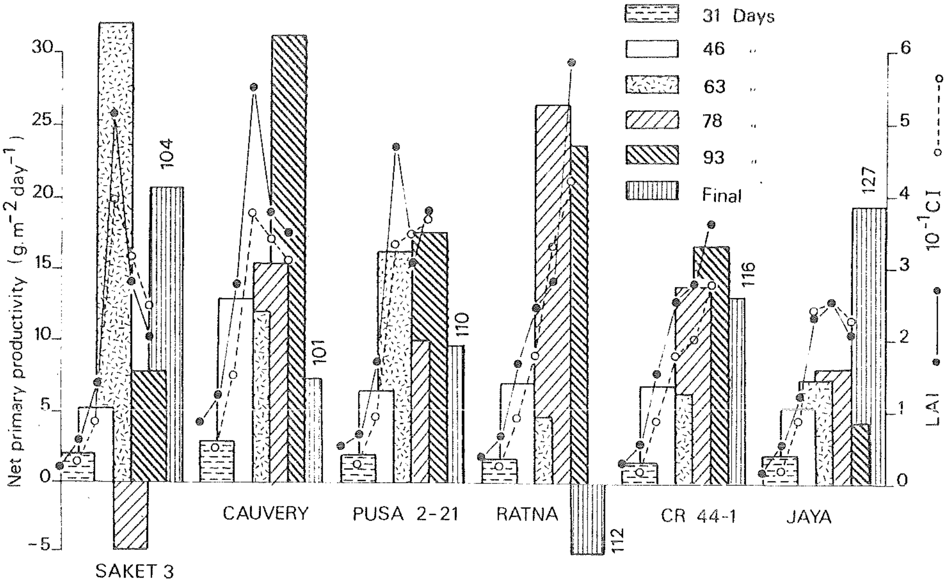

Fig. 1 : Variation in net primary productivity, LAI and chlorophyll index (CI) with age in six varieties of rice grown under rain-fed upland conditions.

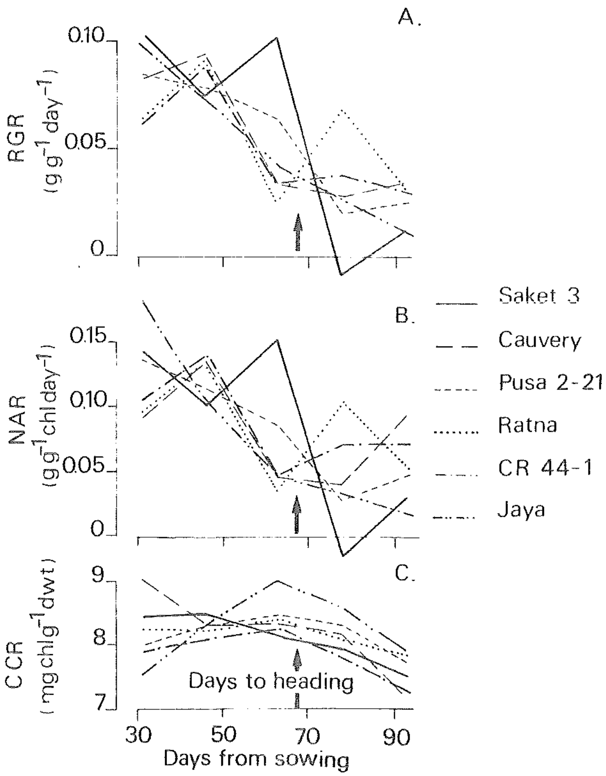

Fig. 2 :

Time course of a) RGR, b) NAR and c) Chlorophyll content ratio (CCR) in six varieties of rice grown under rain-fed upland conditions. Days to heading, indicated by arrow except for Jaya, were 65 in Cauvery, 66 in Saket 3, 67 in Pusa 2-21, Ratna, CR 44-1 and 96 in Jaya.

Relative growth rate.

RGR reached its peak in all the varieties during the vegetative growth period (Fig. 2 a). In Pusa 2-21 and Jaya, the peak occurred a fortnight earlier, i.e., by the 31st day after sowing, than in the other varieties. Having attained the peak, RGR declined subsequently with age. An upswing in RGR was, however, observed during the post-earing phase in all the varieties.

Net assimilation rate.

NAR closely followed the trend of RGR in all the varieties (Fig. 2 b) yielding a highly significant positive correlation (Fig. 3). In general, the peak rate of net assimilation was attained during the vegetative stage but the time differed with the variety. Pusa 2-21 and Jaya registered their peak at the 31st day; Cauvery, Ratna and CR 44-1 at the 45th day; while in Saket 3 it was recorded at the 63rd day, almost towards the end of the vegetative phase. The highest peak value was obtained by Jaya (0.018 g mg^{-1} Chl d^{-1}), followed by Saket 3 (0.015), CR 44-1 (0.014), Pusa 2-21 (0.014), Ratna (0.013) and Cauvery (0.013). Having attained the peak, NAR declined with age. A conspicuous recovery in NAR, however, occurred during the early earing stage in Ratna and CR 44-1, and during the mid post-earing phase in Saket 3, Cauvery and Pusa 2-21. In the case of Jaya, NAR fell consistently from the 31st to 95th day, beyond which further evaluation of the parameter was dropped due to increased leaf rolling and suppressed ear emergence.

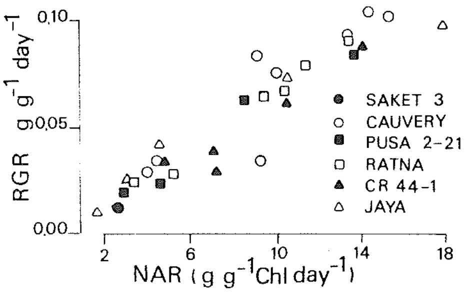

Fig. 3 : Relationship between RGR and NAR in rice. The data represent six varieties at five ages.

Variety	Pre-heading net assimilate ($g\ m^{-2}$)	Post-heading net assimilate ($g\ m^{-2}$)	Ear dry weight ($g\ m^{-2}$)	Filled grain (%)	Dry matter allocated to ear: % of current net assimilate	% of pre-heading reserve
Saket 3	678	257	444	86	100	28
Cauvery	498	727	595	76	82	nil
Pusa 2-21	464	208	266	59	100	13
Ratna	334	554	298	42	54	nil
CR 44-1	307	99	92	21	93	nil
Jaya	489	603	60	10	10	nil

Tab. III : Varietal variations with regard to allocation of pre- and post-heading net assimilates to the economic compartment in six rice varieties under rain-fed upland conditions.

Chlorophyll content ratio.

In general, CCR tended to form a parabolic curve with age of the crop (Fig. 2 c). It neither showed a close association with RGR nor with NAR.

Leaf area index.

Statistical analysis for varietal difference in LAI was not significant. Leaf area expansion was relatively faster in Saket 3, Cauvery and Pusa 2-21, attaining maximum LAI just prior the ear emergence (Fig. 1). In the remaining varieties expansion of leaf area continued steadily up to the late post-earing stage. The highest LAI was attained by Ratna (5.63), and the other varieties followed in the decreasing order of Cauvery (5.52), Saket 3 (5.16), Pusa 2-21 (4.71), CR 44-1 (3.69) and Jaya (2.54).

Chlorophyll index.

CI followed closely the trend of LAI, except at 78 days in Pusa 2-21 where it decreased unlike LAI. The varieties fell under two groups with respect to their CI. The first group comprising Saket 3 and Cauvery, showed more or less a parabolic trend with time, attaining their peak just before flowering. The second group including the other four varieties, presented an almost linearly increasing trend until leaf senescence set in (Fig. 1). Maximum CI was reached by Saket 3 at 63 days coinciding with the peak of NAR and productivity.

Pre- and post-heading net assimilate allocation to the ear.

Table III reveals that in Saket 3 and Pusa 2-21 the entire post-heading net assimilate was accumulated in the ear. In addition, a substantial amount of dry matter in them was also remobilised from the pre-heading reserve to the ear. Cauvery and Ratna, which lagged behing Saket 3 during pre-heading, produced two times greater post-heading net assimilate, but not all of it was allocated to the ear. Jaya also produced the post-heading net assimilate more than twice of Saket 3, but the dry matter allocated to the ear was only 5.4 % of the total. CR 44-1, on the other hand, poured the entire post-heading net assimilate into the ear but the amount of assimilate produced was far less in comparison to the other varieties.

DISCUSSION

A study of the morphological characters of the present varieties reported earlier (SINGH, 1976) revealed that Saket 3 and Cauvery had a superior yielding potential than the other cultivars under drought conditions. Crop duration was found to be negatively correlated with grain weight and percentage of filled grains. A time series analysis of calorific distribution pattern in these varieties has also supported the yielding superiority of Saket 3 and Cauvery (SINGH, 1975). The varieties differed both in the structural as well as functional attributes with time and developmental stage, which possibly brought forth the differences in their biological and economic yield.

The relationship of the growth function, RGR, with its components NAR and CCR reveals that RGR is more dependent upon NAR (Fig. 2) than on CCR. Productivity on the other hand, reflected a combined effect of LAI/CI and NAR. The maximum of NAR did not always coincide with the maximum of LAI/CI, and possibly due to this the dry matter production pattern varied among the varieties. The highest productivity achieved by Saket 3 at 63 days, just prior to earing, may thus be attributed to its peak NAR attained in synchrony with peak LAI and CI. Cauvery and Pusa 2-21 also reached maximum LAI and CI preceding earing, but a simultaneous decline in their NAR limited their productivity. In Cauvery, however, a considerable rise in NAR during the post-earing phase, after 78 days when a fairly high LAI and CI still persisted, boosted up the productivity to its peak at 93 days. Conversely, relatively lower productivity in CR 44-1 and Jaya may be attributed to the noncoincidence of peak NAR with maximal LAI and CI. Thus, synchronization of size (LAI and CI) and efficiency (NAR) of the photosynthetic system at a desirable growth stage through breeding may be an effective approach in increasing the dry matter production efficiency of a variety. NAR reached its peak prior to earing in all the varieties and declined thereafter. However, it showed upswing either during early (Ratna and CR 44-1), or mid (Saket 3, Cauvery, and Pusa 2-21) post-earing phase suggesting a revival in photosynthetic activity at grain formation time. A rise in NAR during post-earing phase could be of significance as grain weight is largely dependent on the current photosynthesis (YOSHIDA, 1972; SUZUKI, 1975). An upswing in NAR during the seed ripening phase has also been reported in some other crops (KOLLER *et al.*, 1970; CLARKE & SIMPSON, 1978). KOLLER *et al.* (1970) have attributed the increase in NAR to the response of the photosynthetic apparatus to increased demand for assimilates by the rapidly growing seeds. The timing of upswing in NAR during post-earing phase also seems to have an important bearing on grain filling. Ratna and CR 44-1 recording an increase in NAR during early post-earing phase had lower grain weight in comparison to Saket 3, Cauvery and Pusa 2-21 in which the upswing in NAR occurred during the mid post-earing phase.

Saket 3, which expressed the best economic yield potential, grew slowly until 46 days from sowing, but following production of large leaf area and chlorophyll content by the 63rd day, in time with maximum NAR, its biomass surpassed that of the other varieties. More than 50 % of the total biomass in Saket 3, as also in Pusa 2-21 and CR 44-1, was produced before the onset of earing. It has been observed that a variety with greater pre-heading reserve is more capable of withstanding dry spells occurring during post-earing phase (SOGA & NOZAKI, 1957; RACKHAM, 1972). In a drought susceptible variety, translocation of carbohydrates from the assimilatory sources and pre-heading reserve from the culms to the economic sink is often retarded by drought resulting in poor economic yield (LAHIRI, 1956). The present experimental period perchanced to fall in an atypical drought year. Water input during the post-earing phase in particular was only 17 % of the total input (423 mm) to the crop. Moreover, a severe drought spell spread from the 89th day onward when the varieties were in the grain ripening stage. Despite the severity of drought, remobilization of photosynthates to the ear in Saket 3 was less affected than in the other varieties. This is evident from the fact that all the post-heading net assimilate was allocated to the ear, and in addition a substantial proportion (42 % of the grain weight) was drawn from the pre-heading reserve also, resulting in a high percentage of filled grain. In Cauvery, Ratna and Jaya, on the other hand, post-heading net assimilate was much greater than the pre-heading, but inability of the latter two to mobilize it sufficiently to the economic sink resulted in a large number of poorly filled grains. Cauvery, however, appeared superior to Ratna and Jaya in utilizing the post-heading net assimilate for grain filling and produced a high percentage of filled grains next only to Saket 3. Pusa 2-21 resembled Saket 3 in accumulating the entire post-heading net assimilate in the ear, but a relatively small pre-heading reserve of which only 13 % was remobilized to the ear seems to have limited grain filling. Similarly in CR 44-1, although the proportion of post-heading net assimilate allocated to the ear was higher than that in Cauvery, low assimilate production limited economic yield.

A significant correlation obtained between the relative amount of chlorophyll in the ear at grain-filling time and ear to plant weight ratio at maturity is of some interest as it suggests contribution of ear-photosynthesis towards grain-filling. A relatively higher concentration of chlorophyll in the ear of Saket 3 and Cauvery may to a certain extent have contributed to higher percentage of filled grains. LOOMIS *et al.* (1971) have reported about 20 % of the grain weight in rice by the panicle itself. The self supportive capacity of ears towards grain filling in rain-fed rice in particular could be of significance as mobilization of photosynthates to the ear from the other source is impeded by drought. In one of their experiments on *Brassica napus*, CLARKE and SIMPSON (1978) found a significant correlation between maximum pod areas and yield under rain-fed conditions as against a non-significant correlation in well irrigated plant. Further experimental evidence is however necessary for confirmation of self contribution of ear towards yield in rice under rain-fed conditions.

The phasic developmental pattern of rice varieties under rain-fed conditions to express optimal yield potential may be in many respects different from that of the varieties adapted to wet conditions. An extended period between heading and maturity, as suggested by TSUNODA (1964), may be advantageous for increasing yield under favourable environmental conditions, but under areas prone to drought, the chances of the variety succumbing to drought may increase (SINGH, 1976). Thus, a variety of short duration with intensified pre-heading growth, like Saket 3, seems to be advantageous for a better grain yield under rain-fed conditions. Nevertheless, an active mobilization of pre-heading reserve to the ear remains a major concern for the economic success of a variety.

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