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EFFECTS OF PLANTING DENSITY ON WATER USE AND PRODUCTIVITY OF PEARL MILLET (*PENNISETUM TYPHOIDES*) GROWN ON STORED WATER. I. GROWTH OF ROOTS AND SHOOTS

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SUMMARY

Pearl millet (*Pennisetum typhoides*) was grown on stored water at Niamey, Niger, using three row spacings (38, 75 and 150 cm), to determine the physiological basis of exploitation and conservation of water by crops during drought. Between 18 and 32 days after sowing, roots grew rapidly beneath all crops reaching 140 cm in the narrow spacing, but there were differences between crops in the pattern of growth. Soil cores and trench profiles indicated that plants in wider rows had fewer, deeper roots. Substantial differences in both the amount and pattern of shoot growth were recorded in the different populations. Initially growth was fastest at the narrow spacing but stopped by day 45 and eventually the wide spacing produced most dry matter due mainly to greater survival of tillers. The partitioning of above ground dry matter into vegetative and reproductive fractions was similar at all three spacings and was consistent with figures for comparable crops elsewhere. The important role of tillers is discussed in relation to the development and maintenance of a canopy.

It has long been recognized that the yield of crops growing in dry environments is very dependent on water supply. To obtain the maximum yield, the plant population and planting pattern must optimize the use of water available in the soil. Agronomists are therefore interested in identifying the optimum populations for particular areas, and many such trials have been reported in this journal. However, if the principles of the relation between population and water use were more clearly understood, then it ought to be possible to predict the optimum spacing for given edaphic and climatic environments.

In temperate regions it has been established that the production of dry matter by crops is largely dependent on the interception of radiation (Monteith, 1977). This conversion of radiant energy to chemical energy is dependent upon the area of intercepting surface and the conversion efficiency. During drought stress, either or both of these factors may be affected (Legg *et al.* 1979). A model developed by Ryhiner and Matsuda (1978), simulating the effects of population and water supply on wheat production, indicated that the surface resistance of the leaves played a dominant role in determining final yield. More

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recently, Babalola and Oputa (1981) studied the changes of leaf resistance caused by altering the planting density of maize.

This paper and its sequel (Azam-Ali *et al.* 1984) report on an experiment to determine how the water supply available to a crop in the soil interacts with the atmospheric demand for water in determining dry matter production. Drought is difficult to guarantee in the field without recourse to shelters, but by growing crops in a tropical post-rainy season it is possible to control the amount of water available by irrigation. Different populations of plants were used as a means of changing the accessibility of soil water during growth in a period when the chance of rain exceeding 15 mm was less than 5% (Virmani, Reddy and Bose, 1980). This paper describes the growth of roots and shoots of three populations of semi-dwarf pearl millet *Pennisetum typhoides* (S & H) growing on stored moisture; its sequel analyses the results in relation to water use and the interception and efficiency of conversion of radiation to dry matter.

SITE, CROP AND SEASON

The experimental area was an almost flat, 0.4 ha plot on the farm of the World Meteorological Office Agrhymet Centre, Niamey, Niger (13° 29′ N, 2° 10′ E). The soil was a deep sand, free of stones, overlying finer material of the past floodplain of the River Niger which now flows about 1.5 km to the north of the site. Measurements showed that the top 1 m of soil was physically similar throughout (99.5% coarse and fine sand; bulk density 1.51 g cm^{-3}), although at the southern edge of the experiment finer alluvial material came to within 40 cm of the soil surface. The top 1 m of soil had an available water capacity of 67 mm between tensions of 5 kPa and 1.5 MPa. As the crop grew, marked differences in growth across the area were evident; statistical implications of this are discussed later.

Ten days before sowing, a compound fertilizer (15:15:15) was broadcast by hand on the area at a rate of 200 kg ha^{-1} and rotavated into the soil. Two days before sowing, the soil was irrigated using sprinklers to bring the moisture content in the top 2 m of soil close to field capacity. On 18 October 1980, pearl millet (cv BK 560) was sown by hand in east/west rows at three different row spacings (38, 75 and 150 cm) by placing six to ten seeds in shallow holes 20 cm apart along the rows. A light irrigation was applied immediately after sowing to promote emergence, which occurred within two days.

Initially, the experimental design was a randomized block design replicated four times, with each block (37.5 m x 25 m) containing a 14 row plot of each spacing. However, shortly after germination, considerable damage was done to two blocks by crickets and the design had to be changed. The remaining two blocks were halved to give four new blocks each 37.5 m x 12.5 m. This loss of blocks meant that a standard statistical analysis of the results was invalid. In the results that follow, mean values of all four new blocks are given but no standard errors because firstly, the individual values were not true replicates, and secondly, of the four values frequently two were high and two low (i.e. the four individual values were not normally distributed about the mean). However, analysis of variance at 45, 59 and 86 days after sowing (DAS) using the true number of replicates (two) rather than the four that had been used showed that on all occasions treatments were significantly different ($p < 0.05$) and replicates were not, while block effects were significant only at 86 DAS. In summary, using only four values to estimate the mean does not alter the conclusions of this study and, as will be seen from the results, there were clear differences between treatments and internal consistency between sequential measurements within any particular treatment.

Because of the infestation by crickets, the crop was dusted almost daily for the first 12 days with benzene hexachlorene (Lindane) and well irrigated to encourage growth. Urea (45 kg ha^{-1}) was applied to the crop at 12 DAS and irrigation stopped at 15 DAS. The crop was thinned in stages between 10 and 20 DAS to leave one plant every 20 cm along the row, giving established mean populations of 2.9, 5.8 and 11.5 plants m^{-2} for the 150, 75 and 38 cm row spacings, respectively.

There was no rain during the experiment and the weather was almost continuously hot. Daily mean temperature was 30°C at the start of the experiment, decreasing to between 22° and 23°C in December; class A pan evaporation between 0600 and 1800 h ranged from 5.2 to 6.2 mm. A dust haze obscured the sun on some days in mid-November and by mid-December remained close to the ground for many days.

SAMPLING

Shoot growth

Plants were harvested every week between 17 and 73 DAS (except at 66 DAS) and a final harvest was taken at 86 DAS. At 17 DAS, ten plants were removed during the thinning of each plot, but at 24 and 31 DAS, two 1 m samples from adjacent rows were removed from a similar position in each plot. At subsequent harvests the procedure was changed because of the considerable variability of growth within plots. From 38 DAS onwards, two rows at the edges of the plots were left intact and groups of ten plants, each at least 2 m apart, were taken randomly from the remaining rows.

Plants were pulled out of the soil and then cut at the point where the uppermost root emerged. In the laboratory, the number of leaves on main stem and tillers was recorded for each plant, together with the number of emerged panicles. The sample was then divided into two; half of the plants were dried intact and the remainder partitioned into leaves, stems and panicles of both main stems and tillers before drying. Green area was also determined; the length and width of leaves were measured with a rule and their area calculated by treating the leaf as a rectangle where its edges were roughly parallel, and as a triangle at the tip. Lengths and breadths of stems were also measured and the stem area calculated assuming the stem to be a cylinder; for consistency with laminar area, stem areas were taken as half that calculated.

Root growth

During early growth only, roots were measured by two techniques, to give the vertical distribution of length and dry weight, and an assessment of spatial distribution. Cores of soil were extracted on three occasions (17, 24 and 31 DAS) from the narrow spacing and once (38 DAS) from the medium and wide spacings. A Jarratt auger, 10 cm in diameter, was used to extract disturbed cores of soil in 10 cm increments to a depth of 100 cm; below this depth, a 5 cm diameter auger collected samples in 20 cm increments to the maximum sampling depth of 140 cm. At each sampling, one core was taken from each plot from the middle of a row in the narrow and medium spacings and from a quarter of the way across the row in the wide spacing. The roots were washed from the soil, organic debris removed, and root length measured using Tennant's technique (Tennant, 1975). Dry weight was measured afterwards.

Spatial distribution of roots was assessed using the 'trench profile' technique (Bohm, 1977). Trenches spanning almost four rows of the crops were dug to a depth of 70 cm at the eastern edge of one block. The eastern faces of the trenches were covered with polythene sheets to prevent evaporation. At each measurement (18, 25 and 32 DAS), the east faces were advanced by at least 30 cm to within 5 cm of the base of a plant. The face was smoothed and washed with water, a wire grid of 2 cm squares placed against it and the number of cut root ends in each square counted.

RESULTS

Shoot growth

The maximum green area index (L) was reached in the narrow spacing by 31 DAS, in the medium by 38 DAS, and in the wide by 45 DAS (Fig. 1). Thereafter, leaf area decreased in the same sequence so that at 73 DAS, the wide spacing had the largest L. Although the maximum number of leaves on the main culm was 13 or 14, irrespective of treatment, senescence of both main culm and tiller leaves was more rapid in the medium and narrow spacings than in the wide. The figure also indicates the greater contribution of tillers to total L in the wide spacing during later growth. By 73 DAS, stem area was a major component of L in all treatments and accounted for 43% of the green area of the narrow spacing.

The rate of dry matter accumulation per unit ground area was different in the three spacings and was initially slowest for the wide spacing (Fig. 2). Between 31 and 59 DAS, however, the rate of growth at the wide spacing was almost constant and by 73 DAS the wide spacing had the greatest dry weight. Increase in dry weight in the medium and narrow spacings ceased at 59 and 45 DAS respectively. By 73 DAS, the weight per plant in the wide spacing was more

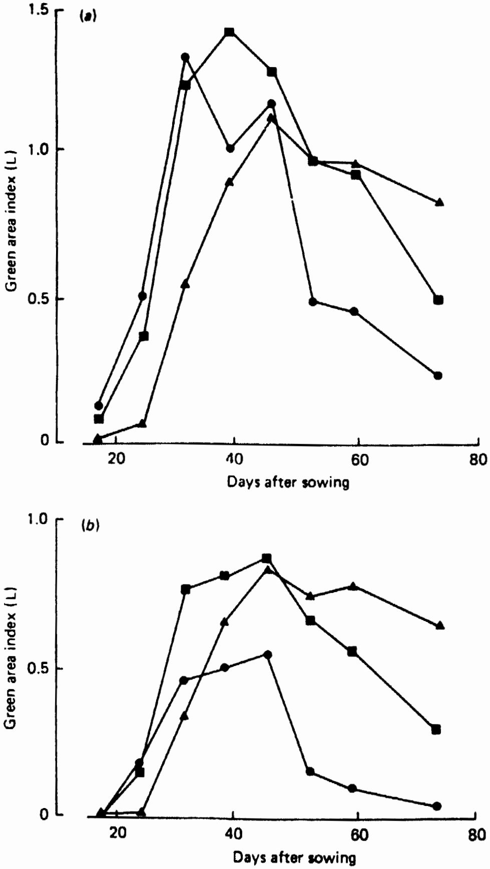

Fig. 1. Changes in green area index (L) of (a) the whole plant and (b) the tillers; (●) narrow, (■) medium and (▲) wide spaced millet.

than twice that in the medium and eight times that in the narrow spacing. The effect of few plants per unit ground area in the wide spacing was thus more than offset by the heavier individual plants that resulted from increased tillering and better tiller survival. At 59 DAS, tillers represented 75% of the total shoot weight in the wide spacing, 66% in the medium spacing but only 21% in the narrow spacing.

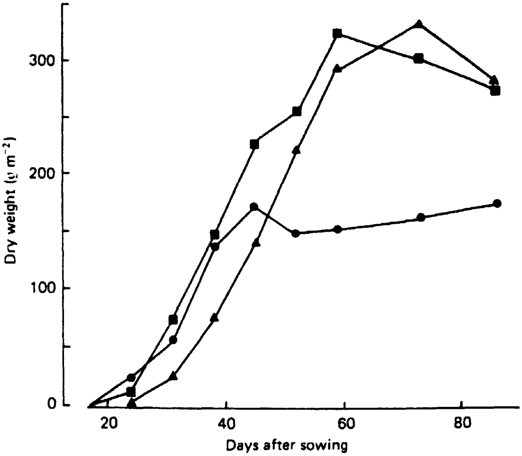

Fig. 2. Shoot dry weight for narrow (●), medium (■) and wide (▲) spaced millet.

Flowering was completed by 45 DAS at all spacings but occurred slightly earlier in the narrow and medium spacings. In the wide spacing, almost all the increase in shoot weight after flowering was accounted for by the increase in panicle weight (Fig. 3a). From 73 DAS the increase in panicle weight was associated with a declining stem weight. In the narrow spacing, panicle weight increased from 45 DAS largely at the expense of stem weight (Fig. 3b), a phenomenon also shown by the medium spacing between 59 and 86 DAS (Fig. 3c).

Partitioning of dry matter

The harvest index (panicle dry weight : total shoot dry weight) of the three populations varied between 0.50 and 0.55 over an almost seven-fold variation in plant dry weight (Fig. 4). Similar values of harvest index were measured in crops of the same variety of millet grown in India at ICRISAT in 1977/78 (Gregory and Squire, 1979) at a population of 28 plants m^{-2}. In principle, a minimum amount of dry matter (W_0) must be accumulated before reproductive growth can commence. In practice, W_0 obtained by correlating yield and total shoot weight was not significantly different from zero (-0.55 g). Dry matter accumulated over and above W_0 was partitioned into almost constant vegetative and reproductive fractions irrespective of the final shoot dry weight.

Root growth

Although root dry weights were only determined on three occasions, the limited data indicate a rapid expansion of the root system beneath the narrow

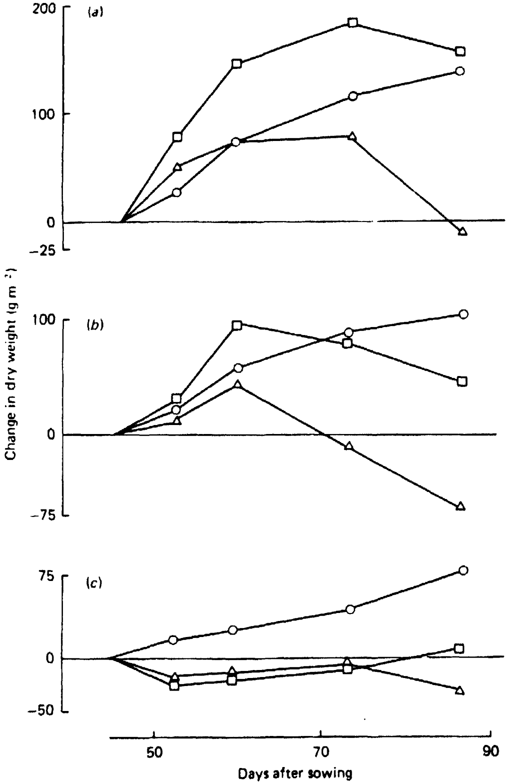

Fig. 3. Changes in dry weight of the whole shoot (□), panicles (○) and stems (△) between 45 and 86 DAS, of (a) wide, (b) medium and (c) narrow spaced millet.

spacing between 17 and 31 DAS (Table 1). The root:shoot ratios are noteworthy for the heavy weight of roots relative to shoots produced in these circumstances.

The maximum depth of root penetration beneath the narrow spacing was 140 cm at 31 DAS (Fig. 5), giving a mean rate of penetration of 4.5 cm per day and a rate between 17 and 31 DAS of 7.1 cm per day. However, there were very few roots below 100 cm. The root densities measured at 31 DAS were similar to those recorded at ICRISAT at a comparable stage of growth (Gregory and Squire, 1979), ranging from about 0.8 cm cm^{-3} at the surface to 0.4 cm cm^{-3} at around 40 cm and then becoming less dense with depth. At both 24

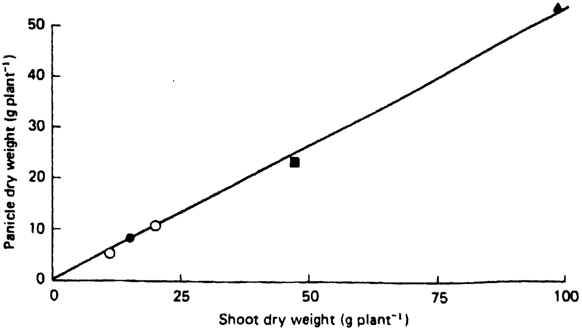

Fig. 4. Relation between dry weight of panicles and shoot dry weight at final harvest (86 DAS); (●) narrow, (■) medium and (▲) wide spaced millet. The two open circles are from measurements made on irrigated and unirrigated crops grown at ICRISAT in 1977/78. All five points fit a constant harvest index of 0.54 (solid line; $r^2 = 0.99$). The variety was BK 560 throughout.

and 31 DAS, root density was less between 30 and 40 cm than at some greater depths. The reason for the increased root densities at around 40 cm is unknown; the soil profile was texturally similar throughout, and no impeding layers were present. The total root length at 38 DAS in the wide spacing was only about half that in the medium spacing (Fig. 6), as was also evident in individual soil layers.

The trench profile technique also demonstrated the rapid growth of roots beneath all spacings between 18 and 32 DAS (Table 2). During the last period of measurement, however, the rate of expansion of the root system of the narrow spacing appeared to be slow in comparison with other spacings. A simulated display of root distribution measured with the trench profile technique was obtained using a computer; an example of the distribution at 32 DAS is shown in Fig. 7.

At 18 DAS, the roots were visible as discrete groups confined to the individual plants and restricted to the upper 5 cm of soil but by 25 DAS the root systems of all crops had extended considerably. Roots had grown to meet between rows in the surface layers but marked differences in downward penetration were evident. The narrow spacing had many root axes below 30 cm

Table 1. *Changes in root dry weight and root:shoot ratio during the early growth of narrow spaced pearl millet*

Days after sowing	Root dry weight (g m^{-2})	Root:shoot ratio
17	5.7	1:1.14
24	25.4	1:0.96
31	29.9	1:1.46

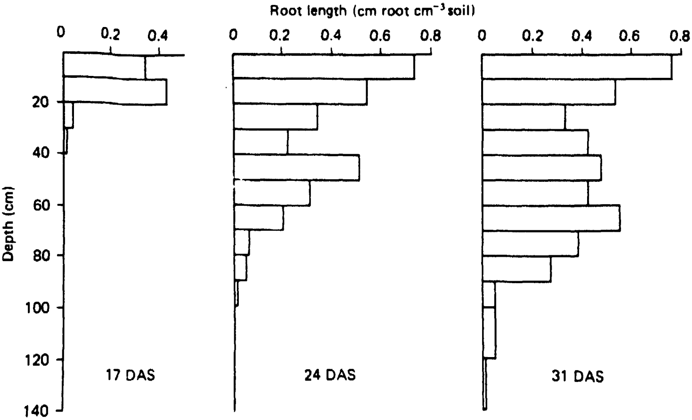

Fig. 5. Distribution of millet root length with depth beneath the narrow spacing at 17, 24 and 31 days after sowing (DAS).

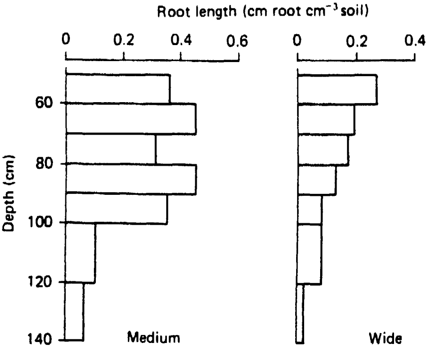

Fig. 6. Distribution of millet roots deeper than 50 cm beneath medium and wide spacings at 38 DAS.

Table 2. *Total number of roots between rows of millet, measured using the trench profile technique*

	Spacing		
Days after sowing	Narrow	Medium	Wide
18	59	37	†
25	457	222	281
32	597	580	751

† Not measured.

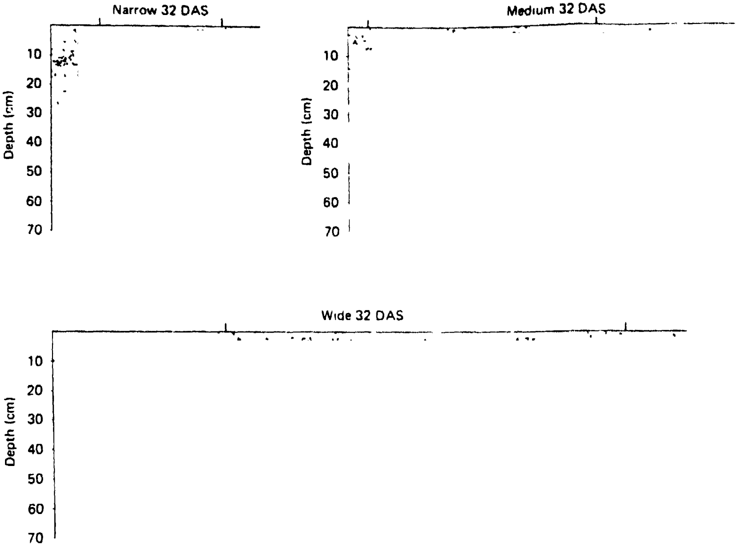

Fig. 7. Millet root distribution at 32 DAS determined by the trench profile technique. The position of plants is indicated by a line.

producing short, lateral roots; at the other extreme, most of the roots of the wide spacing were confined to the upper 20 cm. The rooting pattern in the medium spacing was intermediate in nature with some roots below 30 cm but most above 20 cm. In both narrow and medium spacings, the layer of soil between 15 to 25 cm had fewer roots than the layers immediately above and below.

By 32 DAS, further root growth had occurred in all crops in most layers of the profile. Growth in the narrow spacing was confined to the upper 25 cm and a smaller number of roots was observed below this depth than before. It is unlikely that death of roots had occurred at this stage of growth so spacial variability is the most likely explanation. Nevertheless, there still were most roots at the narrow and fewest at the wide spacing.

DISCUSSION

For many temperate crops, the relation between growth, yield and population is well known. Many workers have confirmed the hypothetical relations of Shinozaki and Kira (1956) and Holliday (1960), who first postulated that total dry matter per unit ground area approaches an asymptote at the planting density at which the canopy intercepts radiation almost completely. Further increase in population has little effect on dry matter production but yield per unit area may decline at extremely high populations because of inter-plant competition and the failure of very small plants to produce a yield.

The validity of these responses has rarely been considered for tropical crops especially those growing with a finite supply of water. The Dry Land Farming Research Scheme (1982) has shown that yields of sorghum are influenced by both population, site and season in a complex manner. This experiment, at a single site, explored in detail the growth and final yields resulting from the balance between exploitation of water reserves by roots and conservation of water by reduced transpiration.

The weight of roots in the narrow spacing at 31 DAS (about one week before anthesis) was similar to the value of 38 g m^{-2} at anthesis measured by Gregory and Squire (1979) in India, but our root to shoot weight ratio is much higher. In temperate regions, roots of cereal crops (e.g. wheat) are usually 10 to 25% of the dry weight of the whole crop, but in this experiment the value was closer to 50% - an unexpectedly large figure. Samples may have been unrepresentative but the results were backed up by the trench profiles and are consistent with Russell's (1977) comments on the increased root growth of crops in dry environments.

The results shown in Figs 6 and 7 suggest that the distribution of roots was affected by spacing and that fewer roots grew deep into the profile beneath the wide spacing. The rapid downward growth of roots in the narrow spacing (7.1 cm a day) implies a rooting depth at anthesis of about 2.2. m. Since there is usually no substantial root growth after anthesis, this depth of penetration probably represents the limit of extractable water.

The development of sufficient leaf area to intercept incident radiation fully is often regarded as a prerequisite of maximum yield in temperate regions. In dry regions, the capacity to intercept radiation has to be balanced against the desirability of conserving water. The present results show that changed spacing had a significant effect on the expansion and survival of leaf surface. Results published elsewhere (Azam-Ali, 1983) indicate that L was the main determinant of evaporation from the three spacings, having a far greater influence on seasonal water use than other physiological factors, (e.g. stomatal resistance), or physical factors (e.g. vapour pressure deficit). The maximum L of the narrow spacing (1.4) was small in comparison with the figure of 2.2 achieved by a similar crop of millet grown in irrigated conditions (Gregory and Squire, 1979). The role of tillers in regulating leaf area in dry conditions appears to be paramount. The physiological consequences of this regulation are discussed in our second paper (Azam-Ali *et al.* 1984) but its effects on growth were clear; in the narrow spacing very few tillers survived to produce panicles whereas in the wide spacing they provided most of the yield.

Finally, although a crop may stop increasing in weight as a result of drought, growth of the reproductive organs may continue. In all the spacings, there was evidence for translocation of assimilate from the stems, a process which provides another mechanism for ensuring survival in drought-prone environments.

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