In the eastern part of India, the cultivated rice *Oryza sativa* has two wild relatives namely, *Oryza nivara* and *Oryza rufipogon*. *O. nivara* is an annual and grows in dryland aerobic habitats compared to the perennial *O. rufipogon* that lives in less aerobic swampy habitats. Tillering is generally more restricted in the *O. nivara* than *O. rufipogon*. Both environmental parameters and genotypic variation determine tiller number and dynamics of rice in the field (De Datta, 1981; Yoshida, 1981). However, the stability of tiller hierarchy among genotypes across a range of growth habitats and the relationship of tiller dynamics and hierarchy with the assimilate concentration of their panicle are not known. In this study, the natural habitat of these two species has been altered to simulate cultivated conditions in order to assess the impact of environmental conditions on the mechanism of assimilate partitioning between different types of tillers and determination of tiller number.

**Materials and Methods**

1. **Plant materials and natural habitat**

Two species of wild rice namely *O. nivara* L. and *O. rufipogon* Griff growing in their natural habitats around the Sambalpur University campus (21.25°N; 83.52°E; altitude 160 m) in the wet season of 2002 were used in the experiment. The weather conditions and fluctuations in water depth of the habitats are given in Fig. 1. *O. nivara* is annual, mono-tiller, erect, 90 cm tall, photo-insensitive upland rice adapted to non-flooded aerobic sandy loam soil containing N, P and K at the ratio of 4.3: 5.24: 90.7 kg ha\(^{-1}\) in the natural habitat. The soil was collected 10 inches deep from the surface at three different locations. It bears a small panicle. *O. rufipogon* is prostrate, multi-tiller, perennial; large paniced photo-sensitive deep-water rice of elongating type adapted to submerged sandy loam soils (surface to 10 inches deep) containing N, P and K at the ratio of 5.8: 6.44: 116.2 kg ha\(^{-1}\) and rising water levels.

2. **Cultivated conditions**

Thirty days old seedlings of both species with uniform growth and development were carefully dug out from their natural habitat and transplanted into cement pots (330 × 330 × 260 mm) containing 42 kg of sandy loam soil and farm yard manure (ratio 3:1) in open field conditions. These pots were arranged in a randomised block design with three replicates. Plants were grown at a density of 36 plants m\(^{-2}\). Commercial N, P and K were applied at a ratio of 80:17.6:35.6 kg ha\(^{-1}\) in split doses. The water level in the pots was maintained at 5 ±2 cm except one week after transplanting and before maturity.

3. **Sampling**

Plants with uniform growth and development were tagged (by leaf count and similarity of height) for both species in three locations in their natural habitat and these plants were sampled at random on different occasions. Sampling was initiated from the time of tiller emergence and continued up to maturity at 7 day intervals. On each sampling occasion, one plant from each of location was uprooted and carefully washed. The individual tillers of the plant were separated and height, leaf area and dry weight of plant parts were recorded. Similarly, the plants in the pots were marked for uniform growth and development and sampled in the same manner as in the natural habitats. Not more than one plant from a pot was sampled on any occasion.

4. **Morphological and biochemical measurements**

The dates of emergence, panicle initiation, booting, anthesis and maturity of each individual tiller of the plant were recorded. The tillers were identified with reference to the leaves subtending them on the culm (Fig. 2). The panicles of different types of tillers were...
severed from the neck node at booting, anthesis and maturity and put immediately into an oven for estimation of dry weight. The dried panicle was boiled in 80% aqueous methanol and the extract was used for the estimation of sugars (Buysee and Merck, 1993) and amino acids (Yemm and Cocking, 1955), and the residue was used for starch estimation (Buysee and Merck, 1993).

Results

1. Morphological features

The dryland species *O. nivara* attained flowering and completed its life cycle much earlier to that of the lowland species *O. rufipogon* in their natural habitats (Tables 1 and 2). This difference was almost retained when the species were grown in the pots. *O. nivara* was mono-tillering in the natural habitat, but produced 27 tillers under the cultivated conditions. In contrast, *O. rufipogon* had 3 primary and one secondary tillers in its natural habitat, but produced 7 primary, 16 secondary and 15 tertiary tillers under the cultivated conditions. Most of the tertiary tillers were sterile. In both species the duration of growth of the tillers declined acropetally with successive nodes of the stem of the main shoot, primary and secondary tillers because the maturity date of all tillers was similar. Habitat did not influence this hierarchy. Panicle initiation, anthesis and maturity times were delayed considerably when *O. nivara* was transplanted

![Graph showing water level and meteorological conditions](image)

Fig. 1. Water level in the lowland and dryland habitats during the months of July to November 2002 (a) and the meteorological conditions during the period of the experiment (b).

![Diagram of rice plant tillers](image)

Fig. 2. Tillers in the rice plant. M, Main shoot; P, Primary; S, Secondary and T, Tertiary tillers. P1 is the first primary tiller on the axil of the second node of main stem and P2, P3 etc. are found on the subsequent nodes. Similarly, P1S1 is the first secondary tiller on the first node of P1, and P1S2 is the second. P1S1T1 is the first tertiary tiller of the P1S1 tiller. The other tillers are named accordingly.
### Table 1. Phenological features of *Oryza nivara* under cultivated and natural conditions.

| Tillers        | Days after tiller emergence | Dry weight at MA (g) | Panicle length at MA (cm) | Growth duration (days) |
|----------------|-----------------------------|----------------------|---------------------------|------------------------|
|                | TE  | PI  | AN  | MA  | Shoot | Panicle | Veg.  | Rep.  | Total |
| Cultivated habitat |     |     |     |     |        |         |       |       |       |
| M              | -   | 61  | 74  | 90  | 5.50±0.21 | 1.53±0.02 | 27.22±0.60 | 70   | 29   | 99    |
| P1             | 0   | 62  | 75  | 90  | 4.39±0.19  | 1.41±0.03  | 27.01±0.39  | 62   | 28   | 90    |
| P3             | 5   | 62  | 75  | 90  | 3.80±0.02  | 1.29±0.09  | 26.24±1.40  | 57   | 28   | 85    |
| P6             | 10  | 63  | 76  | 90  | 2.46±0.01  | 1.10±0.01  | 25.53±1.10  | 53   | 27   | 80    |
| P1S1           | 8   | 62  | 75  | 90  | 3.60±0.14  | 1.35±0.01  | 26.91±0.59  | 54   | 28   | 82    |
| P1S3           | 14  | 65  | 78  | 92  | 3.09±0.09  | 1.00±0.01  | 23.11±0.87  | 51   | 27   | 78    |
| P2S1           | 10  | 62  | 75  | 90  | 3.40±0.01  | 1.31±0.02  | 26.05±1.90  | 42   | 28   | 70    |
| P2S3           | 16  | 66  | 78  | 92  | 2.90±0.03  | 0.99±0.01  | 23.01±0.48  | 50   | 26   | 76    |
| P3S1           | 14  | 65  | 77  | 92  | 3.06±0.02  | 1.14±0.02  | 25.92±1.20  | 51   | 27   | 78    |
| P6S1           | 17  | 66  | 78  | 92  | 2.40±0.01  | 0.70±0.01  | 23.32±0.70  | 49   | 26   | 75    |
| P1S1T1         | 23  | 68  | 79  | 93  | 1.30±0.12  | 0.41±0.02  | 22.11±0.40  | 45   | 25   | 70    |
| Natural habitat |     |     |     |     |        |         |       |       |       |
| M              | -   | 49  | 62  | 75  | 0.54±0.11  | 0.54±0.01  | 26.62±1.57  | 55   | 26   | 81    |
| P1             | 0   | 52  | 65  | 77  | 0.39±0.07  | 0.51±0.02  | 20.11±0.92  | 52   | 25   | 77    |

TE, tiller emergence; PI, panicle initiation; AN, 50% anthesis; MA, maturity; Veg., vegetative; Rep., reproductive; M, main shoot; P1, first primary tiller; P6, sixth primary tiller; P1S1, first secondary tiller emerged from P1; P2S1, first secondary tiller from P2; P6S1, first secondary tiller from P6; P1S1T1, first tertiary tiller from P1S1 and so on. ± Values represent the standard deviation of three replicates. For tiller terminology, refer Fig. 2.

### Table 2. Phenological features of *Oryza rufipogon* under cultivated and natural conditions.

| Tillers        | Days after tiller emergence | Dry weight at MA (g) | Panicle length at MA (cm) | Growth duration (days) |
|----------------|-----------------------------|----------------------|---------------------------|------------------------|
|                | TE  | PI  | AN  | MA  | Shoot | Panicle | Veg.  | Rep.  | Total |
| Cultivated habitat |     |     |     |     |        |         |       |       |       |
| M              | -   | 84  | 97  | 132 | 13.23±0.32 | 1.62±0.01 | 27.31±0.89 | 101  | 48   | 149   |
| P1             | 0   | 85  | 97  | 132 | 11.12±0.45 | 1.62±0.02 | 27.13±0.47 | 85   | 47   | 132   |
| P3             | 7   | 86  | 98  | 132 | 09.12±0.35 | 1.59±0.02 | 26.41±0.09 | 79   | 46   | 125   |
| P6             | 14  | 89  | 100 | 133 | 06.85±0.44 | 1.43±0.01 | 25.84±1.30 | 75   | 44   | 119   |
| P1S1           | 11  | 86  | 98  | 132 | 09.15±0.42 | 1.59±0.01 | 26.52±0.43 | 75   | 46   | 121   |
| P1S3           | 20  | 90  | 101 | 133 | 05.12±0.11 | 1.10±0.01 | 23.12±1.09 | 70   | 43   | 113   |
| P2S1           | 12  | 87  | 99  | 132 | 08.15±0.14 | 1.55±0.02 | 26.15±0.78 | 75   | 45   | 120   |
| P2S3           | 22  | 91  | 102 | 134 | 04.89±0.12 | 1.05±0.01 | 23.91±0.29 | 69   | 43   | 112   |
| P3S1           | 15  | 90  | 100 | 133 | 07.88±0.24 | 1.53±0.01 | 26.02±0.89 | 75   | 43   | 118   |
| P6S1           | 19  | 91  | 102 | 134 | 03.18±0.05 | 1.43±0.02 | 25.13±0.83 | 72   | 43   | 115   |
| P1S1T1         | 21  | 93  | 104 | 134 | 02.45±0.11 | 0.39±0.01 | 24.91±0.30 | 72   | 41   | 113   |
| Natural habitat |     |     |     |     |        |         |       |       |       |
| M              | -   | 85  | 105 | 119 | 08.03±0.12 | 1.37±0.06 | 26.90±1.20 | 98   | 44   | 142   |
| P1             | 0   | 87  | 106 | 119 | 06.84±0.10 | 1.36±0.01 | 26.71±1.40 | 87   | 42   | 129   |
| P2             | 2   | 88  | 107 | 119 | 05.50±0.06 | 1.24±0.15 | 26.22±1.05 | 86   | 41   | 127   |
| P3             | 5   | 90  | 107 | 119 | 05.13±0.07 | 1.22±0.02 | 26.01±1.50 | 85   | 39   | 124   |
| P1S1           | 8   | 91  | 111 | 120 | 04.82±0.10 | 1.20±0.01 | 25.82±1.10 | 83   | 39   | 122   |

TE, tiller emergence; PI, panicle initiation; AN, 50% anthesis; MA, maturity; Veg., vegetative; Rep., reproductive; M, main shoot; P1, first primary tiller; P6, sixth primary tiller; P1S1, first secondary tiller emerged from P1; P2S1, first secondary tiller from P2; P6S1, first secondary tiller from P6; P1S1T1, first tertiary tiller from P1S1 and so on. ± Values represent the standard deviation of three replicates. For tiller terminology, refer Fig. 2.
Plant height, leaf area and biomass of panicle and conditions. Both species increased significantly in the cultivated of transplanting did not consistently affect the phenology into the cultivated conditions, but the effect of Table 3. Soluble carbohydrate and starch concentrations of different categories of tillers of two wild species of rice O. nivara (left) and O. rufipogon (right) at anthesis and maturity grown under cultivated and natural habitats.

| Tillers | O. nivara | O. rufipogon |
|---------|-----------|--------------|
|         | Sugars (μg mg⁻¹ dwt) | Starch (μg mg⁻¹ dwt) | Sugars (μg mg⁻¹ dwt) | Starch (μg mg⁻¹ dwt) |
|         | Anthesis | Maturity | Anthesis | Maturity | Anthesis | Maturity | Anthesis | Maturity |
| M       | 229.6±11.5 | 045.4±0.3 | 360.9±19.6 | 591.0±11.9 | 166.9±13.6 | 021.2±0.1 | 334.1±13.3 | 542.6±13.0 |
| P       | 166.4±13.9 | 067.7±1.6 | 269.4±14.9 | 535.1±27.8 | 108.5±11.8 | 022.2±0.8 | 276.8±12.4 | 486.5±20.6 |
| S       | 104.6±15.6 | 147.4±4.4 | 207.0±24.9 | 466.8±16.4 | 086.5±10.8 | 059.1±1.8 | 246.8±24.3 | 453.2±36.4 |
| T       | 037.5±0.1 | 38.0±2.8  | 083.5±2.40 | 137.0±11.5 | 040.0±0.29 | 48.8±4.2  | 073.6±09.4 | 109.2±11.4 |

|         | Anthesis | Maturity | Anthesis | Maturity | Anthesis | Maturity | Anthesis | Maturity |
|---------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| M       | 134.3±8.3 | 089.1±1.1 | 109.7±8.9 | 391.7±13.9 | 138.1±12.4 | 082.0±0.8 | 186.3±6.8 | 472.6±11.2 |
| P       | 111.5±9.0 | 102.0±0.6 | 089.3±4.8 | 348.1±0.80 | 093.1±10.5 | 11.5±1.7  | 161.6±7.2 | 442.8±09.9 |
| S       | −         | −         | −         | −         | 083.9±0.59 | 14.8±0.6  | 154.5±7.8 | 431.5±10.1 |

M, main shoot; P, primary tiller; S, secondary tiller; T, tertiary tiller. ± Values represent standard deviation of three replicates.

3. Assimilates and starch concentrations of the panicle
The concentration of sugars in the panicle of the main shoot, primary and secondary tillers increased rapidly between booting and anthesis stages in both species and under both habitats and declined thereafter to maturity (Table 3, data for booting not shown). The concentration declined acropetally among tiller nodes. However, unlike the situation in other tillers, the concentration of sugars in the panicles of tertiary tillers was not as low at maturity and was comparable to the concentration at booting and anthesis. The fluctuation in the concentration of free amino acid of the panicle was mostly similar to that of the sugars (data not shown). Unlike assimilates, the concentration of starch of the panicle increased with passage of time in all the tillers. The starch concentration of the panicle was higher in a basal tiller compared to that of an apical tiller. In both species, the concentration of starch in the panicle was significantly higher in the cultivated condition compared to the natural system (Table 3).

Discussion
Cultivated rice Oryza sativa originated from wild progenitors like Oryza nivara and Oryza rufipogon during the course of evolution and diversified into a wide range of ecosystems worldwide (Cook and Evans, 1983). The morphology and phenology of ecotypes vary significantly with variation of the habitat. Tilling capacity of an ecotype is one of the morphological attributes that can be considered as an indicator of a plant’s adaptation to its habitat. A high tilling rate at the early stage of growth has been proposed to be due to the abundance of resources (Dingkuhn and Kropff, 1996), and constraints of resources can limit tiller number. In the present experiment, the tiller number differed considerably between the ecotypes of the two species of wild rice when cultivated in contrasting habitats. The dryland species O. nivara produced only one tiller in addition to the main shoot in its natural habitat, which lacked ponded water. However, it became profusely tilling in the cultivated system due to alleviation of water and other physico-chemical...
Compared to *O. nivara*, tiller number of *O. rufipogon* was relatively higher in its natural habitat and the variation in tiller number was not as much evident when both the ecotypes were grown in the cultivated agro-ecosystem. Water logging in the habitat of this ecotype (Fig. 1) might have created a reducing environment in the soil, thereby increasing the concentrations of exchangeable form of many essential elements like nitrogen, phosphorus, potassium, iron, manganese and silicon (Yoshida, 1981). In the wetland system, adequate water supply could also be responsible for sustaining a larger number of tillers in *O. rufipogon* compared to *O.nivara* growing in the dryland. It is opined that phenological adaptation is achieved by progressively adjusting the life cycle of the crop to the particular environment and in the process stress effects are minimized (Evans, 1984).

In our experiment, plants in the cement pots, bereft of environmental stresses, not only increased tiller number, but also significantly increased the biomass of the vegetative and reproductive structures of the tillers in both species. The change in phenology was more evident for *O. nivara*, than that of *O.rufipogon* because natural habitat of the former was more disturbed than the latter.

It is proposed that the physiological processes and functionality of the morphological changes in reaction to environmental factors must be explored to find out the adaptive plasticity of the plants and their evolution (Blom, 1999; Sultan, 2001). In our study, the presence of a high concentration of assimilates at the time of anthesis and starch at the time of maturity in the early-formed tillers indicates the metabolic dominance enjoyed by these tillers over their late-formed counterparts. Soluble assimilates accumulated in the panicle of some of the late-formed tertiary tillers because they might not be able to convert them into starch (Table 3). These observations indicate that both species possess genotypic potential for production of a large number of tillers, but phenotypic expression...
of this potential is limited by the capacity of assimilate production due to the deficiencies of nutrients and water in the growing conditions of the habitat. In cereal crops, the availability of assimilates largely influences ear development (Gallagher et al., 1976) of the tillers. Competitions for assimilate among tillers (Aspinall, 1962; Lafarge et al., 2002) and other organs (Mohapatra et al., 2004) influence availability of assimilates in the panicles. The competition can increase when assimilate supply is limited due to the limited size of the source area in newly formed tillers which senesce earlier than older tillers (Masle, 1985). In our study on the wild rice, the time of maturity and duration of reproductive growth of tillers remained identical, but the duration of vegetative growth decreased in an acropetal fashion along the stem, the duration correlated positively with vegetative and reproductive features of the tillers (Fig. 3). We conclude that the hierarchy of tiller development in rice could be influenced by competition for assimilates within the tillers during the reproductive stage. Poorer vegetative growth in a succeeding tiller compared to that of the preceding tiller makes it less competent to partition assimilates in favour of panicle growth. Since tillers are largely independent in their assimilate budget (Dingkuhn and Kropff, 1996), the competition exacerbates and becomes more acute with the increase of tiller order on the culm and decrease of tiller age due to the progressive decline of source area. We assume that the tertiary tillers became deficient in growth hormones and reached maturity early resulting in an inability to utilise assimilates. We conclude that the tillering capacity of the two *Oryza* species studied is largely physiological and genetic limitations are less important in a cultivated habitat. The dryland species *O. nivara* could not accumulate rainwater given its environment and subsequent sub-optimal growth conditions restricted biomass production. The plant adapted to these conditions and rapidly progressed through its life cycle through low biomass production and high reproductive allocation (Oka and Morishima, 1997). No tillers developed in the succeeding nodes of the main shoot or the primary tiller due to the limitation of resources. Conversely *O. rufipogon* evolved in the more stable environment of a lowland habitat, which ensured its survival for longer duration and production of many tillers. The study also revealed the close phylogenetic relationship between the two species of *Oryza*, due to the similarities of phenotypic plasticity in response to diversity of soil moisture regime. In the flood plains of Asia, soil moisture regime fluctuates drastically due to erratic monsoons and undulated land topology. Populations of rice might have differentiated in response to diverse moisture regimes across the gradation of habitats (Sato, 2000). Differentiation led to speciation; the annual mono-tillering type *O. nivara* in the disturbed dryland habitat and the perennial multi-tillering type, *O. rufipogon*, in the relatively stable environment of lowlands (Oka, 1991).

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