Review Article

Plasticity of Tiller Dynamics in Wild Rice *Oryza rufipogon* Griff.: A Strategy for Resilience in Suboptimal Environments

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Rice cultivation in tropical Asia is susceptible to drought and flood and the need is high for stress resistant genes. Wild rice *Oryza rufipogon* Griff., grows in close sympatric association with cultivated rice in various habitats across the globe and possesses traits for survival under challenging environments. The species adapts according to the level of soil moisture available and modifies phenology, biomass production and grain yield. Variation in tiller dynamics of the species between contrasting environments gives an estimate of the adaptation. The species possesses AA genome, which permits genetic compatibility for cross breeding with cultivated rice. Utility of the species as possible repository of stress resistant genes is evaluated in this review by examining variation in assimilate partitioning between different classes of tillers of ecotypes growing across a gradation of habitats against background knowledge available for cultivated rice. Models have been constructed to explain mechanisms of tillering and tiller dynamics, and reveal the genotypic permissibility for resilience in sub-optimal environments. It is concluded that environmentally cued alteration in assimilate production and partitioning mask genetic potential for tiller production and survival. Tiller number in excess of resource capacity is corrected by senescence of late-tillers possibly through an ethylene-mediated signal.

1. Introduction

The *Poaceae* family of monocot angiosperms constitutes of grasses which provide food and fodder for man and other animals on earth. In this family, contribution of the genus *Oryza* is of high economic importance to man and domestic animals. This genus consists of two cultivated species, namely *Oryza sativa* L. and *Oryza glaberrima* Steud and 20 other related non-domesticated species [1]. *Oryza* species are related more to the bamboos [2] than to other cereals [3]. Hence for cultivated rice, the wild species of *Oryza* are the only source for useful traits for genetic recombination. Vaughan [1] divided the *Oryza* species into two major complexes, such as *O. sativa* and *O. officinalis* (also *O. latifolia*) on the basis of genomic diversity. The cultivated species of rice belong to the former complex along with non-domesticated species like *O. nivara* Sharma et Shastry, *O. rufipogon* Griff., *O. barthii* A. Chev, and *O. longistaminata* Chev. et Roehr. *O. meridionalis* Ng. Species belonging to this complex possesses AA genome group and 24 chromosomes. The genomic group of the species of the second group is BB, CC, DD, and EE in plants with diploid chromosome number or a combination of any two in plants of tetraploid chromosomal constitution. Lack of genomic relationship with cultivated rice has made *O. officinalis* complex less attractive for scientific manipulation of gene flow from the wild to domesticated rice. In contrast, species belonging to the *O. sativa* complex have been assessed for enrichment of gene pool for higher grain yield and resistance for biotic and abiotic stresses. Compared to the other wild species, *O. rufipogon* is studied more extensively for its compatibility of genetic introgression into the cultivated rice *O. sativa*. Incidence of natural intercrossing between the two species is very high resulting in establishment of numerous morphological intergrades [4]. Several authors have considered *O. rufipogon* progenitor of *O. sativa* [5–7].
2. Morphological Diversity of Oryza rufipogon

2.1. Habitat of Oryza rufipogon. Oryza rufipogon grows in close sympatric association with Oryza sativa by occupying the same agroecosystem used by the latter. It competes vigorously and successfully for growth with the cultivated rice. The seeds shatter to ground before maturity and contribute nothing to the overall grain yield. Its infestation in cultivated rice fields puts pressure on essential resources like fertilizers, water, and incident light. Phenotypic similarity of the species with cultivated rice during vegetative growth period precludes its identification and eradication before flowering. The species survives both as wild and weedy races; human support is essential for completion of life cycle of the latter, while the former survives naturally in the wild habitat with no anthropogenic intervention.

Similar to the cultivated rice, Oryza rufipogon is semi-aquatic and phytoecography of the species is strongly influenced by soil moisture regime. Level of soil moisture, depending on land topology, rainfall pattern, and other climatic conditions has dictated phenology, biomass and grain yield of the species growing under various environmental conditions across the world. The species is a native of Asia, but in course of diffusion, it has migrated to some parts of North and South America, Oceania, and Africa [8]. The species grows on a wide diversity of ecosystems ranging from summer—parched dry land to permanent water holes like pools and ditches holding stagnant or slow running water. The altitude of the habitats ranges between 0 to 1000 m.

2.2. Phenotypic Plasticity. Adaptation to such a wide spectrum of diverse ecological conditions exhibits the extraordinary capacity of Oryza rufipogon for resilience in aberrant climatic conditions resulting in origin of new ecotypes, land races, species, and ultimately the cultivated rice. The wide margins of diversification of the species bear testimony to the history of domestication of cultivated rice O. sativa, which is the most important food crop on earth today. Utility of the species has been warranted further, because the presence of potential stress resistant genes/trait ensures successful completion of life cycle under uncertain climatic pattern that may induce erratic weather conditions in the forthcoming decades due to excess rainfall and rising atmospheric temperature. Plasticity of phenotypic architecture in response to habitat deterioration is evident within the ecotypes or land races collected from various ecological habitats. Cultivated rice has also adapted itself to the divergence of land habitats similar to Oryza rufipogon. Nevertheless, these cultivars or land races adapted to different habitats have become recalcitrant or obligatory to the ecosystem concerned and lost the capacity for growth in any environment other than their own. In contrast ecotypic divergence between landraces or ecotypes of Oryza rufipogon, although very drastic, has been flexible and exhibits potential for progressive evolution.

Ecotypes living in summer—parched dry land are annual, and they are not seen in those parts of Asia, where summer is mild. They germinate and establish a high density of population briskly after receiving a good soaking rain fall at the end of summer season in the tropics. High intensity of allelopathic competition for limited resources causes elimination of most of the individuals of the population. Only a few of the population survive and reach maturity. The plants in such unstable environment often support only one tiller. Early flowering shortens the period of vegetative growth, and harvest index is relatively high because of the preference for reproductive growth. At maturity, a few seeds are produced in the panicle. The seeds ripen early and are prone to shattering. Compared to the cultivated rice, seed development on the panicle is more asynchronous, grain yield is low, the seed dormancy period is higher, and spikelets are more deciduous [7]. Elongated lemma bearing a long pointed awn helps seed anchorage in the moist soil. Sharma and Shastry [9] assigned a separate identity (species) for the annual form of Oryza rufipogon, that is, Oryza nivara, and Oka [7] and Khush [5] corroborated it later. It is suggested that the cultivated rice O. sativa had its origin from the annual form of O. rufipogon species in course of domestication. Phylogeographic studies of the wild rice [10] and genic noncoding microsatellite marker studies of the domesticated rice cultivar groupe [11] indicated that cultivated rice was domesticated twice from different populations of O. rufipogon in Asia. The products of these two independent domest ications were indica and japonica subspecies of O. sativa; the former was domesticated in the Indian peninsula, while the latter was domesticated in Indo-China. The indica-japonica differentiation of O. rufipogon was considered a result of adaptation to different environments [12]. Contrary to this view, Kovach et al. [13] found evidence for multiple domestication of rice, but it was concurred that the indica and japonica subspecies arose from genetically distinct gene pools within a common wild ancestor Oryza rufipogon. Because O. rufipogon is a perennial species, its annually occurring form, O. nivara may be the immediate precursor of the domesticated rice. Both the species, however, belong to the same ancestral gene pool.

The perennial form of O. rufipogon is a native of permanent water holes in the undulated flood plains of Asia. Compared to O. nivara, O. rufipogon lives in a stable and more favourable environment [1]. In the swampy marshlands, the plant elongates its stem quickly in response to accumulation of monsoonal flood water; stem elongation continues until stability of water level at the end of monsoon period. The plant expresses strong ratooning ability. Fibrous roots emerge from the nodes of the submerged stem part. The level of water recedes in the postmonsoon period, and the stem sleeps over the ground. New tillers regenerate from the nodes of the rhizomatous stem, which is the primary mode of propagation. The plant is strongly photoperiodic and flowers at the advent of winter season. The period for seed development is very short as starch filling is completed within a short span of 10 days [14]. Reproduction by seed production is rare, and there are only a few seeds in the inflorescence. They shed easily to the ground and remain viable and dormant up to 3 years. The change of phenotypic expression leading to possible ecotypic divergence of O. rufipogon in response to adaptation to different water regimes across a toposequence has been demonstrated in Vaughan [1].
3. Variation in Tiller Production

3.1. Tiller Production an Indicator for Adaptation. Compared to self-breeding *O. sativa*, both *O. rufipogon* and *O. nivara* are relatively more cross-pollinated. There is natural cross pollination between the cultivated and wild rices resulting in formation of numerous intergrades between the two species [4]. Reports of interspecific hybrids between cultivated rice *O. rufipogon* and *O. nivara* are also available in the literature [15]. The hybrids diverge across a variety of habitats and establish themselves into new ecotypes. When temperature is conducive for growth, it is the soil moisture regime, which determines the nature of adaptation. The presence of such highly variable range of weedy perennial or annual non-domesticated rice types often creates taxonomic confusion. It is not easy to study the genetic make up of a large number of wild or cultivated *Oryza* species and establish phylogenetic relationship between them. Therefore, study of morphological characters comes in handy in such situation. Pang and Wang [16] used several phenotypic traits like morphological features, ratooning ability, mode of reproduction, and nature of seed dormancy for classification of a large number of wild rice types in China.

The wild or weedy rices are superior competitor to cultivated rice. They possess early vigour, establish large number of tillers, and reach greater stem height [17]. These traits are essential for adaptation and survival in natural ecosystem, where the plant has access to favourable environment for a limited period only. But the features contribute to a heavy burden on farmer’s economy in the cultivated condition; the superiority of vegetative growth helps wild rices to produce more number of tillers and outpace growth of the cultivated species. Given advantage of the plentiful resources of a manipulated agroecosystem, profuse tillering feature of wild rice helps better utilization of space for biomass production. In high yielding semidwarf rice, early and high tillering capacity is considered beneficial for grain yield [18, 19]. Thus, tiller dynamics in rice is an important indicator not only for the nature of adaptation to environment and primary production but also for reproductive growth and grain yield. The restriction of tiller production in a rice genotype indicates adverse influence of a suboptimal environment, while profuse tiller production accounts for optimum growth under favourable environment.

3.2. Growth of Tillers. Tiller growth in wild rice has not been studied precisely. Because of close alliance, tiller production in wild rice is not expected to be different from that of the cultivated rice. In cultivated rice, tillering is an important agronomic trait for grain production. Tiller determines the plant architecture and canopy development for capture of incident light for primary production. Tillers are branches that develop from the leaf axils on the nodes of main culm or other tillers during vegetative growth [19]. The initiation of reproductive growth coincides with node elongation, and hence, elongated nodes do not bear tillers. On the main culm, emergence of the fifth leaf coincides with that of the first leaf of the tiller from the axil of second leaf, and emergence of sixth leaf coincides with the first leaf of tiller coming out at axil of the third leaf. It suggests that growth of the *n*th leaf of main culm is synchronous with that of the first leaf of tiller coming out of the *n*-3 leaf [19].

The tillering stage starts with the appearance of first tiller from axil of the second leaf of the main culm. The coleoptile and first leaf nodes do not bear tillers [19]. In each tiller, development of prophyll, which corresponds to the coleoptile of main culm, precedes emergence of the first leaf. The prophyll is small and whitish, and lacks a leaf blade. It remains enclosed within the leaf sheath of the main culm and not visible. After emergence, a tiller gains independence from the enclosure of preceding leaf sheath; it develops fibrous roots and establishes capacity for own primary production.

Primary tillers develop from the main culm in an alternate order. After emergence, primary tillers produce secondary tillers in the same order. Secondary tillers bear a third group of tillers; the tertiary tillers. The production of tertiary tillers begins at the end of secondary tiller production. Tertiary tiller production continues up to the maximum tillering stage [18]. Some of the later-formed tiller buds die or remain dormant. A schematic of rice tillers is given in Figure 1.

3.3. Asynchronous Growth of Tillers. In rice tiller number is an important attribute for grain yield, but all tillers produced in the plant are not productive. Tillers originate on culm nodes in an acropetal succession. The hierarchy in tiller development becomes evident as grain yield becomes poorer in each successive tiller [20, 21]. Thus, increasing the number of later-initiated tertiary tillers does not contribute much to the final grain yield. The early-initiated primary tillers possess higher sink-source ratio, spikelet number, and leaf area per tiller, sink capacity, and filled grain percentage [22]. The number of vascular bundles decreases in an acropetal sequence among the tillers. The primary tillers emerging from the basal nodes of main culm possess larger number of vascular bundles compared to the tertiary tillers originating later on apical nodes [23]. Poor vascularity in the tertiary...
tillers decreases supply of assimilates and hormones from the source leaf to the reproductive parts, and thereby, restricts grain filling [24]. Padmaja Rao [25] reported that reduction in partitioning of biomass to the reproductive parts decreases harvest index of the later-initiated tillers. Additionally, the duration of vegetative and reproductive growth of the later-initiated tillers are short because phenological events like tiller emergence, booting, and anthesis are delayed in them but maturity date is more synchronized [26]. Therefore, the leaf area becomes relatively smaller in later-initiated tillers to sustain reproductive growth and grain yield, and grain quality in them becomes poorer [27, 28]. Conversely, the early-initiated tillers establish dominance in assimilate partitioning at crucial stages of grain development like booting and anthesis for the benefit of grain yield [26]. In the NPT rice, apical dominance is encouraged during the vegetative stage to restrict tiller number and it is reduced during reproductive stage in order to increase panicle size and grain number [29].

4. Tiller Dynamics of Oryza rufipogon in Contrasting Environments

As discussed, the tiller dynamics of rice is an important agronomic trait of high significance for grain yield. There exist significant genetic differences in number of tillers among the rice cultural types. Apart from the genetic diversity, spacing, level of irradiation, nutrient supply, depth of soil, field water regime, and cultural practices influence tillering and tiller development of rice [18, 19]. Effects of environmental or genetic factors on tillering being so explicit however, the ecophysiology of tillering or tiller growth are not understood properly. A similar problem also exists in grain sorghum [30]. Li et al. [31] have opined that tillering in rice can be used as a model system for studying branching pattern in monocotyledon plants. It is known that the wild rice Oryza rufipogon is amenable for change in response to environmental perturbations. Therefore, compared to the cultivated rice types, which are recalcitrant natives of their own cultural conditions, Oryza rufipogon provides a better clue for the alteration of phenotypic expression in response to environment diversification. Using random amplified polymorphic DNA marker, the genetic diversity of the species was tested and found to be high among topologically segregated populations in Kerala, India, recently; and maintenance of the purity of the wild gene pool was recommended for conservation and future improvement of cultivated rice [32]. However, the limits of genotypic permissibility for change of phenotypic expression in tillering in response to environmental diversification have not been studied adequately.

Kariali et al. [33] tested the pattern of tiller dynamics of Oryza rufipogon growing in deep water marshy situation and its dry land ecotype (often called Oryza nivara [1]), in response to a changeover from their natural habitat to the well-managed growing conditions of cemented pots. The deep water and dry land ecotypes had 4 and 1 tillers in their natural habitats, respectively, and the preference was for primary type of tillers. The duration of vegetative growth was very long in the deep water ecotype, while it was short in the dry land ecotype. In contrast, abundance of resources in pot conditions allowed profuse tiller production in both the ecotypes and many of them were the non-productive tertiary tillers. The number of total tillers produced was less in dry land ecotype compared to the deepwater ecotypes grown under the uniform pot condition. Similarly, vegetative growth period of the former ecotype was less in comparison to that of the latter under uniform condition. The experiments revealed the margins of phenotypic permissibility of the ecotypes for tiller production and vegetative growth in response to extreme environments, but the genotypic attributes were not compromised entirely in the process.

5. Physiological Basis of Tiller Dynamics

5.1. Assimilate Partitioning and Tiller Dynamics. In the later half of the nineteenth century, Charles Darwin observed the underlying physiological features of plants growing in diverse environments and the linkage between structures and functions as components of progressive evolution; the spirit continues unabated in modern plant biology [34, 35]. Plants grown under challenging environments modify morphological features because of changes in physiological functions. It is imperative that the physiological processes and functionality of the morphological changes must be explored to understand the nature of adaptation of plants and their evolution [36, 37]. In Oryza rufipogon, Kariali et al. [33] compared assimilate partitioning into the different types of tillers of two ecotypes grown under natural and pot conditions. The objective was to understand stability of tiller hierarchy among the ecotypes across a gradation of growth habitats and the relationship of tiller growth with assimilates concentration of their panicle at different stages of development, because competition for assimilates between tillers [38, 39] and other organs [40] influence availability of the chemical in the panicle of different cereals. Additionally, limited size of leaf area due to poor vegetative growth can exacerbate the competition for a newly formed tiller [41]. In Oryza rufipogon [33], competition for assimilates intensified with the increase of order and decrease of age of tillers as source area progressively declined in a hierarchical fashion from base upwards on the culm. Similarly, poor vegetative growth and source area limited tiller number and growth because of the restricted biomass production and its consequential impact on assimilate partitioning to the reproductive parts. In this study, although tiller dynamics of the ecotypes were largely relegated to the differences in environmental parameters, which influenced assimilate partitioning, the ecotypes strived to conserve and maintain their genetic diversity. This observation corroborates the work of Kato [42], wherein interplant competition within rice hills limited tiller number at high planting density; high population density affected maximum tiller number per plant but not the number of productive tillers. Thus, under aberrant growing conditions, preference in assimilate partitioning is given to older tillers for survival. In the process, development of new tillers is restricted. Sahu et al. [21] found that growth duration, photosynthetic pigments and protein
concentrations of flag leaf and assimilates partitioned into the developing panicle of rice declined acropetally in tillers of successive nodes. A newer tiller on higher node suffered because early senescence limited source area resulting in impairment of assimilates partitioning to the developing grains. Since intertiller transports of metabolites are rare in rice [43], the newer tillers are not able to take the benefit of any supply from older tillers and decimate ultimately. Tiller dynamics, therefore, is resource-dependent and tillering beyond a sustainable number is corrected by senescence.

5.2. Hormonal Control of Tiller Dynamics. The rules of priority among classes of tillers for growth and development [44] were not understood in rice. Early freedom from the physical constraints of preceding flag leaf enclosure may help establishment of large photosynthetic area and metabolic dominance in panicle growth for the older tillers [45, 46]. Because tiller maturity is synchronized, dominance of older tillers can be solely attributed to the difference in time taken for tiller emergence [21], which determines their capacity for primary production. A tiller establishes its independent entity after emergence from the leaf sheath of the preceding leaf. Thus, a multi-tillering plant is a composition of identical number of independent units. It is possible that onset of reproductive growth in the oldest unit (main shoot) cues genesis of a stimulus to induce simultaneous onset of flowering and a programmed process of monocarpic senescence in all tillers borne on it. According to Kariali and Mohapatra [47], the stimulus could be ethylene for rice plant. These workers [47] reported that application of IAA, GA and kinetin regulated diversification of growth and development of temporally and spatially segregated tillers because of their effect on ethylene production. High ethylene production was responsible for reduction of grain yield and growth duration of the later-initiated tillers and kinetin application was beneficial for grain yield. It was concluded that tiller hierarchy of rice could be minimized for increase of grain yield in the older tillers by manipulation of ethylene production. The role of cytokinin in increasing number of branches and spikelets in rice panicle for benefit of grain yield has been corroborated more recently [48, 49]. In a more recent review, McSteen [50] proposed a model for hormones and other environmental factors in tillering and tiller development of monocot grasses.

Strigolactone, a carotene-derived signal (terpenoid plant hormone) discovered recently [51–53], traveling basipetally from the apical bud, inhibits axillary bud growth while cytokinin moving acropetally from roots promotes axillary bud growth. Strigolactone, also travels acropetally out of roots and inhibits axillary bud growth like auxins. Effects of environmental factors on hormones controlling tillering and tiller growth have received poor attention so long. Yan et al. [54] reported that higher rate of tiller production in flooded than in non-flooded soil. It was possible because ACC synthesized in roots was transported upward in xylem to the shoot, where it was converted to ethylene [55]. Under submergence, ethylene concentration increases in plant tissue due to enhanced synthesis and entrapment [56]. High ethylene concentration may be responsible for profuse tillering, because ethylene mediated inhibition of IAA biosynthesis allows promotion of tillering [56, 57] by release of tiller bud growth from apical dominance. It is possible that the wetland ecotype of Oryza rufipogon

Figure 2: Schematic of factors influencing tiller production and development in Oryza species. Arrowhead lines indicate promotion and flat-ended lines indicate inhibition.
produces more tillers than that of the dryland ecotype because soil submergence promotes ethylene production in the former [33]. Unlike ethylene, there is an inverse association between gibberellins action and tillering ability of rice. In deep water rice, the presence of high ethylene promotes gibberellic acid synthesis for rapid stem elongation under submergence [58], which curtails capacity for tiller production. When gibberellic acid synthesis is limited in super rice, it becomes only 30 cm tall but produces as many as 50 tillers [59]. A model projected in Figure 2 explains the physiological factors controlling tiller production.

5.3. Genes in Control of Tillering. Allelic dominance of tillering genes and so the molecular mechanism of tillering are poorly understood in rice. Genetic factors allowing expression for formation of many tillers at vegetative growth stage exacerbates competition for assimilates [43] and slackens growth and grain yield of the late-tillers considerably because of poor morpho-anatomical features for assimilate supply [24]. Genetic manipulation of tillering and tiller formation has been a breeding objective for restriction of tiller number (3-4 productive tillers per plant) in the new plant type of rice [60–62]. Yamamoto et al. [63] reported wide genetic variation in tillering traits in rice cultivars. More than ten quantitative trait loci were found controlling tiller number; the effects of which depend on the stage of tiller development; the QTLs controlling tiller growth at early stage of development were undetectable at later stage of development [64]. Genes causing uniculm phenotype have been identified in rice [65, 66]. On the other hand, profuse tillering attribute has been incorporated into semidwarf high yielding rice [67] for expression of complete grain yield potential [68]. It was reported that a dominant dwarfing gene D-53 controls profuse tillering [69], whereas monoculm 1 (MOCI) regulates control of tillering [31]. Mutant moc1 plant possesses a recessive mutation in a single nuclear location, and it loses tillering ability owing to a defect in tiller bud formation. Zou et al. [70] showed that a recessive htd-1 gene suppresses tillering while Guo et al. [71] found that leafy-head 2 (ihd2) gene reduces tiller number in rice. Similarly, QTL (qTA-9) responsible for tiller angle of rice, has been identified on chromosome 9 of rice [72]. Ying et al. [73] identified expression of three genes related to tiller formation, namely OSH1, MOCI, and OsBT1 in rice and found that a mixture of red and blue light promoted the transcription of the first two genes for enhancing tillering and tiller growth. It is surmised that in rice tillering characters and panicle number per plant are controlled by the genetic system, but expression of the genotype exhibits large environmental fluctuation [42] and consequently has a low heritability.

6. Conclusion

As discussed, there is wide variation of genetic potential for tiller production and survival in rice, but phenotypic expression of this potential is limited by environmental factors controlling intrinsic physiological processes like capacity for assimilate and hormone production. Therefore, genetic limitations for tillering are less important in a cultivated habitat. Variation in tiller dynamics of Oryza rufipogon,
grown under widely contrasting environments provided evidence for this inference [33]. Given its environment, the dry land ecotype (*Oryza nivara*) could not accumulate rain water for induction of tillering and subsequent aberrant growth conditions deprived adequate primary production. The plant adapted to the suboptimal situation; it completed life cycle early through low biomass production and high reproductive allocation [74]. Absence of ethylene in the vegetative shoots restricted tillering and limitation of resources in growing medium precluded sustenance for tiller growth subsequently (Figure 3). Assimilate transport was not maintained to the growing sink of the late-tillers, and they decimated prematurely [26]. Conversely, accumulation of ponded water stimulated ethylene production and tillering thereby, in the wetland ecotype. Ethylene production also encouraged synthesis of gibberellic acid for rapid stem elongation under submergence; stem elongation was responsible for premature cessation of tillering. Wetland habitat was relatively more stable than that of the dry land habitat. However, the genetic potential for tiller production was not completely expressed in the wetland situation because of the higher demand of assimilates in the early-tillers, which elongated faster and accumulated larger biomass than the late-tillers [33]. Besides, there is a positive association between dwarfism and tillering in rice [75]; the dwarf mutants possess large number of tillers [59]. For *Oryza rufipogon* [33], growth conditions were perfectly stable for both the dryland and wetland ecotypes grown in pots; shallow submergence induced ethylene biosynthesis for profuse tillering and adequate supply of nutrition in the growth medium encouraged sustenance of many tillers. Pot conditions allowed expression of full genetic potential of the ecotypes for tillering that was possible neither in the wetland nor in dry land natural situations. Thus, similarities of phenotypic plasticity in tiller dynamics of the ecotypes of *Oryza rufipogon* in response to diversity of soil moisture regime across a gradation of habitats, reveals genotypic permissible for resilience in sub-optimal conditions of growth. This versatile feature is a trait essential for survival under the fluctuating climatic conditions incident presently thanks to global warming. The capacity for tillering and tiller survival of the wild rice is determined by the nature of assimilate production and partitioning; the number of tillers produced beyond resource capacity in an environment is corrected by ethylene-induced senescence of the late-formed tillers.

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