



Review

Senescence, dormancy and tillering in perennial C₄ grassesGautam Sarath^{a,b,*}, Lisa M. Baird^c, Robert B. Mitchell^{a,b}^a USDA-ARS Grain, Forage and Bioenergy Research Unit, Lincoln, NE 68583-0937, United States^b Department of Agronomy and Horticulture, University of Nebraska, Lincoln, NE 68583, United States^c Biology Department, University of San Diego, San Diego, CA 92110, United States

ARTICLE INFO

Article history:

Received 12 August 2013

Received in revised form

13 December 2013

Accepted 15 December 2013

Available online 30 December 2013

Keywords:

Dormancy

Molecular mechanisms

Temperate C₄ grasses

Senescence

Switchgrass

Winter survival

ABSTRACT

Perennial, temperate, C₄ grasses, such as switchgrass and miscanthus have been tabbed as sources of herbaceous biomass for the production of green fuels and chemicals based on a number of positive agronomic traits. Although there is important literature on the management of these species for biomass production on marginal lands, numerous aspects of their biology are as yet unexplored at the molecular level. Perenniality, a key agronomic trait, is a function of plant dormancy and winter survival of the below-ground parts of the plants. These include the crowns, rhizomes and meristems that will produce tillers. Maintaining meristem viability is critical for the continued survival of the plants. Plant tillers emerge from the dormant crown and rhizome meristems at the start of the growing period in the spring, progress through a phase of vegetative growth, followed by flowering and eventually undergo senescence. There is nutrient mobilization from the aerial portions of the plant to the crowns and rhizomes during tiller senescence. Signals arising from the shoots and from the environment can be expected to be integrated as the plants enter into dormancy. Plant senescence and dormancy have been well studied in several dicot species and offer a potential framework to understand these processes in temperate C₄ perennial grasses. The availability of latitudinally adapted populations for switchgrass presents an opportunity to dissect molecular mechanisms that can impact senescence, dormancy and winter survival. Given the large increase in genomic and other resources for switchgrass, it is anticipated that projected molecular studies with switchgrass will have a broader impact on related species.

Published by Elsevier Ireland Ltd.

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1. Introduction

Perennial, warm-season C₄-grasses such as switchgrass (*Panicum virgatum*), miscanthus (*Miscanthus × giganteus*), prairie cordgrass (*Spartina pectinata*) and others are being developed as sources for bioenergy in many temperate regions of the world, due to their many positive agronomic features [1]. In addition to high above-ground biomass yields, these plants also sequester significant amounts of carbon below-ground [2]. In general, these perennial grasses are composed of below-ground tissues, the crowns and rhizomes and roots, and above-ground tillers. A tiller consists of a main stem composed of solid nodes and usually, hollow internodes. Each node subtends a leaf and leaf sheath. Depending on the species, axillary buds present on the nodes may develop into sub-ordinate tillers (branches) [3]. Tiller meristems remain vegetative, and transition into a reproductive phase once appropriate flowering signals are received. Again, depending on the species, plants could contain mostly flowering tillers as in switchgrass, or a combination of vegetative and reproductive tillers, for example, big bluestem (*Andropogon gerardii*). Flowering and seed development generally serve as cues for tiller senescence in cereals and other grasses and could be providing similar cues in C₄ perennial grasses and also could be factors in the induction of dormancy in the rhizomes. Irrespective of these variations in tiller composition, in temperate regions of the world, the onset of winter (first killing frost) will result in the death of the above ground tissues. Crowns and rhizomes and associated tiller buds will stay dormant until spring. Ultimately, all photosynthate required for below-ground growth is derived from the shoots, and the seasonal progression of shoot initiation, growth and eventual senescence of the aerial tissues are intimately linked to growth and the imposition of dormancy in the crowns and rhizomes. Reserves stored in the rhizomes will also drive growth in the spring. Appropriate allocation of reserves in the crowns and rhizomes for maintaining cellular integrity during the dormant phase, for driving the elongation of preexisting tiller buds when growth resumes, and for formation of new meristems, rhizomes and roots during the active growth phase are also likely to influence overall health of the below-ground perennial tissues. As compared to annual plants which are primarily dependent on seeds as their perenniating structures, perennials overcome adverse environmental conditions through maintenance of viable meristems associated with storage organs such as rhizomes, roots, stolons, or other plant structures. Growth of meristems during adverse conditions is detrimental to meristem survival, and thus perennials often have developed mechanisms for inducing dormancy during or prior to the adverse conditions in order to prevent meristem growth. This allows the plant to resume growth with prior stored reserves once conditions are favorable. Seasonal dormancy can occur in the summer months (generally induced by lack of water and/or high temperature) [4–6] or in the winter months (generally induced by low light and low temperature limitation; see below). It is possible that summer dormancy in grasses might share some similar molecular pathways to winter dormancy in temperate C₄ grasses (for example signaling responses to senescence, desiccation, and meristem metabolism). However, mapping these relationships will be dependent on the pace at which the appropriate functional genomic resources and experimental datasets become available for the individual species.

Several excellent papers and reviews have appeared over the last few years that have started to map both the physical and physiological networks that underpin senescence and dormancy, for example see [7–16] to name a few. There appears to be a central role for the clock related genes and in genes regulated by plant hormones (notably IAA, ABA and ethylene signaling) in controlling bud dormancy in the dicot systems. Coordinated regulation of these networks could be critical to ensure timely transition to

dormancy and winter survival. Since these networks are fundamental to plant development, it is likely they will be important circuits in temperate warm-season grasses as well. However, it is also possible that networks unique to these grasses exist based on their developmental and evolutionary history. Redundancy and overlap between these signaling pathways can be expected.

The significant lack of cellular and molecular data on these processes in temperate C₄ grasses is currently a challenge. Meeting this challenge will require detailed biochemical, molecular and cellular analyses of shoots and below-ground tissues collected over a growing season, and harvested from divergent switchgrass populations. Placing changes in gene expression datasets within the framework of plant developmental events (tillering, flowering, senescence, etc.) will yield gene co-expression networks and possibly identify key transcription factors coordinating these vital responses. To identify tissue specific processes required for dormancy induction and release in perennial grasses, similar studies will be needed on the physiology and biochemistry on the different plant organs at these important plant developmental events, along with metabolite profiling of tissues whenever possible. Specific roles of key genes will need to be validated by transgenic routes. These studies can be performed in switchgrass [17,18], but they can be relatively time consuming. Potentially other model systems such as *Brachypodium*, *Setaria italica* and *Panicum halli* could be used which are easier to transform and analyze [19–21]. Ultimately, these datasets will provide genes (targets) and pathways within the developmental biology of the plants that have a strong impact on the agronomic traits of most importance for the sustainable production of biomass from these grasses. Although not considered in this review, there is a large body of literature on other C₄ crop grasses, such as sorghum, sugarcane and maize that can provide additional insights.

2. Impacts of germplasm and harvest management on switchgrass productivity

Under optimal management, currently available switchgrass germplasm can become productive in the first year of establishment and reach full yield capacity in the second year of growth. With appropriate input, specifically N, it is possible to maintain biomass yields for considerable periods of time (>5 years) [22,23]. Under different soil types that have been evaluated, P and K were not as critical as N for maintaining biomass yields, although this can be expected to be soil dependent [24].

The number of times switchgrass and related species can be harvested will be dependent on the genotype × environment interactions. In most parts of the temperate world, current projections are for a single harvest post killing frost, with approximately 50–60% of shoot N remobilized to the rhizomes [25–27]. Under specific conditions, essentially long growing season with reasonable moisture (either through rain or irrigation) can make several harvests possible. Under these situations, the first harvest generally has the highest biomass yields [25]. Although yields are a major driver for production, biomass quality and sustainability of production are important factors as well [25,28]. Lastly, where the effects of repeated harvests during a season on switchgrass stand counts and yield have been evaluated, most studies support a single harvest as an optimal means to maintain stand counts and plant persistence [25,26,29]. Similar scenarios are projected for other target perennial grasses grown in a temperate climate under rain-fed conditions [30]. These data indicate that nutrient cycling from the shoots to the below-ground tissues directly impacts meristems on the crowns and rhizomes, and potentially winter-survival of the plant. In a large-scale analysis of different grasses across the southern half of the USA [31] yield components were dependent on the interactions between the environment and genotype. As an

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