Biennial Crops

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INTRODUCTION

The common environmental signals that regulate the processes of vegetative and reproductive growth cycles in plants are temperature and photoperiod. Mechanisms have evolved in many plants to synchronize reproductive development with a particular environmental cue or cues, thereby leading to improved reproductive success and, therefore, improved fitness. One such adaptation is spring flowering preceded by a season of vegetative growth. Plants with this particular adaptation, or those that require two seasons in order to complete reproductive growth, may be considered biennials.

WHAT ARE BIENNIALS?

Biennials typically consist of a root system, a compressed stem, and a rosette of leaves close to the soil surface following the first season of growth. Biennials generally do not become woody during the second season of growth; however, there are many examples in which root or hypocotyl tissues undergo secondary growth.[1] In such cases, the swollen tissues resulting from this may be used as a crop, such as the hypocotyl and root that are present in the carrot or beet. In biennial plants, food reserves that accumulate in root tissues during the first season of growth are used to produce reproductive structures during the second season of growth. In addition, hormones such as gibberellins and cytokinins are produced in root meristems and transported via the xylem to the shoot, where cell growth and development will occur during this second season of growth.[1]

A number of important crop plants are considered biennial, including cabbage and related *Brassica* crops, sugar beet, Swiss chard, table beet and related *Chenopodiaceae* crops, carrot and related *Apiaceae* crops, onion and related *Alliaceae* crops, and a wide variety of ornamental species. Although many of these plants are considered biennial from a horticultural standpoint, few of them are ''true'' biennials and instead represent genetic modifications for maximization of vegetative growth prior to reproduction. Certain grains that are sown in the fall and flower in the spring, such as winter wheat and rye, may be considered winter annuals. These plants possess a facultative vernalization requirement. Therefore, they will flower more quickly with a cold treatment, but the cold treatment is not required for flowering. Biennials, by contrast, are obligate from a vernalization point of view.

Many cultivated vegetable crops are considered biennials. They are typically consumed after the first season of growth, and thus we usually consider them to be biennials that are cultivated as annuals. This article is largely focused on biennial vegetable crops. Cultivars of most winter annual grain crops are pure lines, and methods of breeding pure lines are discussed in another section. The term ''vegetable'' is problematic from a scientific point of view because it lacks biological meaning and instead refers only to a cultural phenomenon. Still, there are two important criteria for vegetables that allow us to place these crops into a particular category for classification: They are immature plant parts that are of high moisture content. For those vegetable crops that are biennials, the immature plant parts that form during the first season of growth are those that are desired. In fact, it is likely that these organs are the products of artificial selection for enhanced biomass in annual plants.

VEGETABLE CROPS

In the case of many vegetable crops, the large vegetative structures desired by human cultures necessitated longer periods of vegetative growth. Selection under the process of domestication likely modified the life cycle of such crops from annuals to biennials, thereby increasing the vegetative growth period and providing a substantial reserve for subsequent reproductive growth. Three common examples of this are cabbage, carrot, and beet, all of which were likely domesticated from annual ancestors and modified by European agriculturists to adhere to a biennial life cycle.

Cabbage (*Brassica oleracea*) was selected from leafy forms of *Brassica* into a headed form in order to allow for a storage form of this edible plant. Likely, this transition took place as the leafy forms moved from a warm to a cool climate during cabbage domestication. As selection for a headed form was carried out, the life cycle was lengthened to allow for maximal biomass production during the first season of growth. Thus, an annual ancestor was converted

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into a biennial derivative by enhancing vegetative growth at the expense of reproductive growth. The late-summer flowering associated with the annual forms became early-spring flowering in the biennial forms, thereby allowing for only vegetative tissues to be produced during the first season of growth.

A similar evolutionary history took place for the biennial vegetable crops carrot (*Daucus carota*) and table beet (*Beta vulgaris*).[2,3] Annual forms with small root systems were gradually converted to biennial forms as selection was practiced for enhanced root and hypocotyl growth. In the climates where this was practiced, the swollen-rooted forms could be stored for a longer period of time, thereby providing a substantial food source during the winter months.

Table beet has been cultivated for millennia as both a root and a leafy vegetable crop. Its origins trace back to the development of a leafy vegetable by the Romans from wild species of *Beta* growing in the Mediterranean region (reviewed in Ref. [3]). As the crop moved into Northern Europe, the growing season was shorter and the winter was longer. This may have caused selection pressure to favor a transition toward a biennial life cycle by selecting AQ1 a swollen hypocotyl or root as an overwintering propagule. Some have suggested that swollen roots may have been selected from leafy beets cultivated in Assyrian, Greek, and Roman gardens.[4,5]

BIOLOGY OF BIENNIALISM

The term ‘‘vernalization’’ comes from the Latin ‘‘vernus,’’ which means spring. Vernalization is an adaptation to environments in which it is advantageous to flower in the spring, following a season of vegetative growth. Vernalization accelerates the ability of a plant to flower but is not responsible for the formation of flower primordia or for the breaking of dormancy.[6] Vernalization can be obligate or facultative in plants; however, in biennial plants the vernalization requirement is obligate.[6]

Typically, temperatures of 1–7°C are required for adequate vernalization, although many exceptions exist.[6] The duration of the vernalization requirement varies; however, two to three months is average. For many crops, flowering may occur with a minimal period of vernalization, but maximal flowering may require additional time. Some species are sensitive to fluctuations in temperature during vernalization, while others are not.[7] A vernalization treatment can be rendered ineffective with a heat treatment, and this process is known as devernalization. Although seed can be vernalized in some species, most plants must reach a more advanced developmental stage in order to be vernalized. The shoot apex is the most likely spot for the perception of vernalization.[6,8] It is also possible for vegetative tissues to be vernalized and ultimately regenerated into whole plants.

The hormone gibberellic acid (GA) is often implicated in regulating the flowering response in plants. Applications of GA to biennial plants can cause flowering in the absence of vernalization, and this may allow for seed production in a biennial plant during a single growing season. Michaels and Amasino[9] found that the late- AQ2 flowering vernalization-responsive *Arabidopsis* mutants respond normally to cold treatment in the presence of the *gal-3* allele, which is a deletion in kaurene synthase, a gene involved in GA biosynthesis. This finding suggests GA may not be involved directly in the vernalization pathway. Interestingly, the vernalization requirement of a biennial plant can be eliminated by grafting. Non–cold-treated plants can be grafted to cold-treated biennial plants and induced to flower.[8] Lang suggested the possible presence of a vernalization hormone (vernalin) that might be produced constitutively in plants that do not require vernalization as well as in those that do; however, such a hormone has never been identified.

Bolting, or the appearance of a flower stalk during the vegetative growth stage, is detrimental to crop production. Bolting is a fairly common occurrence in early-planted biennial crops such as carrot and table beet, particularly in temperate environments. Significant yield losses can be expected when bolting has occurred, and selection against bolting is routinely practiced. Jaggard et al.[10] reported that 50% of field-grown sugar beet plants bolted when temperatures were less than 12°C for 60 days during vegetative growth. Vernalization typically takes place for 12 weeks during the standard breeding cycle, during which time temperatures are maintained at approximately 2–5°C.

Although seemingly complex from a physiological point of view, biennialism is often controlled by relatively few loci. Both dominant and recessive alleles have been identified that control the biennial versus annual habit. *Hyraceum niger* has a single dominant allele conditioning biennialism, while sugar beet has a recessive allele, *b*, conditioning the biennial habit.[11] Recent work by Michaels AQ3 and Amasino[12] points toward major regulatory genes controlling the response to vernalization and the transition from vegetative to reproductive growth in biennial plants, which is consistent with the finding of a relatively simple genetic control of biennialism.

CONCLUSION

Much of their recent molecular work has been conducted with *Arabidopsis*, a model plant that has shed much light on the biology of biennialism. *Arabidopsis* plants flower in response to long days and vernalization. Many researchers use a rapid-cycling summer-annual ecotype of *Arabidopsis* in their genetic studies. However, many ecotypes of *Arabidopsis* are extremely late flowering unless vernalized, and thus they behave as winter annuals. Two loci, *frigida* and *flowering locus C* (FLC), are responsible for the vernalization-responsive late-flowering habit of these winter-annual ecotypes. The vernalization requirement for late-flowering ecotypes is created when the floral inhibitor FLC is up-regulated. After a cold treatment, FLC transcripts are down-regulated and remain low for the remainder of the plant's life cycle, and it is during this phase that flowering occurs.[12] Interaction and expression of these genes may be responsible for conditioning the biennial habit, and it will be interesting to determine whether biennialism is conditioned by these genes in other species.

ARTICLE OF FURTHER INTEREST

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