Research Reports

Influence of Genotype and Environment on Senescence in Peas, *Pisum sativum* L.

Senescence can be deferred in many plant species by removing developing flowers and fruits. It was this general observation that led Molisch (1938) to ascribe senescence in plants to the mobilizing effect of reproductive organs. This theory, however, is not fully consistent with all the available evidence (Leopold, 1961; 1964; 1967; Lockhart and Gottschall, 1961; Sax, 1962). For example, Krizek et al. (1966) compared paired populations of *Xanthium*, one population induced to flower but debudded and the other population kept vegetative under long day conditions (noninduced). Senescence occurred significantly earlier in the induced plants than in the noninduced plants despite the removal of buds from the former. Senescence, according to recent theories, somehow involves RNA-directed protein synthesis (Osborne, 1962; Leopold, 1961; 1967). Both growth promoters and growth inhibitors are thought to exert their effects by regulating the levels of specific RNAs, and ultimately senescence may be dependent on the balance between growth promoters and inhibitors (Leopold, 1967). A genetic study of several photo-dependent[1] response types of peas (*Pisum sativum* L.) has provided additional information relating to the phenomenon of senescence and is the subject of this report.

Certain pea cultivars show a quantitative lelay in flowering when subjected to short photoperiods, whereas others are insensitive or day neutral, the later varieties being responsive and the early varieties being insensitive (Kopetz, 1938; 1941; Reath and Wittwer, 1952; Paton and Barber, 1955; Hänsel, 1954; Went, 1957; Barber, 1959; Van Dobben, 1963; Rowlands, 1964). In all these studies two basic response classes appear to be involved, the responsive class (here designated as the Kopetz-type or K-type) and the insensitive class (I-type). Despite the differential response to photoperiod, the two types have one character-

[1] The term photo-dependent is used in preference to photoperiodic since in our studies photoperiod and total radiation are confounded and it has not been established to what extent photoperiod alone is responsible for the observed results.
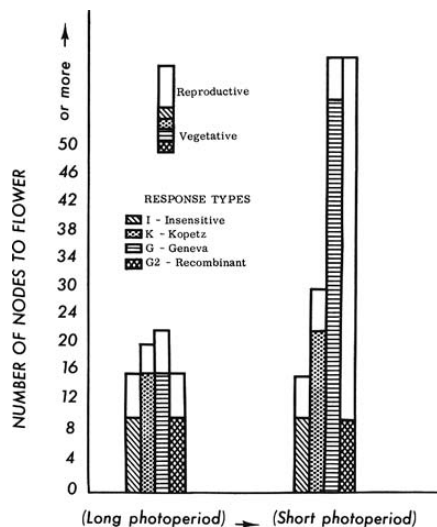

Fig. 1. Vegetative and reproductive behavior of 4 photo-conditioned response types cultivated under long day and under short day conditions (semi-schematic).

istic in common whether grown under LD or SD conditions: once the reproductive phase has begun, the normal train of physiological events ensues and, after a relatively brief period of reproductive development, apical growth ceases, followed soon by senescence and death. Depending on the prevailing conditions, such plants may develop from two to ten reproductive nodes before the apical meristem ceases to function.

Another distinct photo-dependent response class in *Pisum* was found in 1957 by Barton (unpublished) at Geneva, New York. This response type, here designated as the G-type, differs from the K-type by an exaggerated, almost qualitative, response when exposed to SD condition. Inbred line 1326, which expresses the G-type response, may develop from 35 to 85 or more vegetative nodes before flowering when grown under natural short day conditions in the greenhouse during the fall and winter months. Upon exposure to LD conditions, however, line 1326 typically flowers at node 16 or 17; it displays a relatively short period of reproductive development, which, like the K- and I-type plants, is followed by a rapid termination of growth, senescence, and death.

From a cross between the G- and the I-lines we have recovered still another

Fig. 2. Portion of plant cultivated under natural short days in greenhouse showing G2-type response. Abortive flowers appear above and below normal flower.

stable response type, designated here as G2. This type exhibits properties of both parents. Like the I-type parent, the number of nodes to first flower is essentially unaffected by the length of the photoperiod; floral initials characteristically appear at node 10 or 11. Like the G-type parent, however, plants displaying the G2-type response continue to grow for a protracted period of time when cultivated under SD conditions. The four response types are represented diagrammatically in Figure 1.

Plants exhibiting the G2-type response provide evidence antithetical to the theory of Molisch. Under short days such plants may develop as many as 50 or more reproductive nodes, and, although flower and fruit abortion is prevalent during the course of ontogeny (Fig. 2), the number and weight of dry seeds far exceed that obtained from nonresponsive counterparts. At the end of an experiment, some 5 or 6 months after its inception, the G2-type plants develop about the same *total* number of nodes (vegetative plus reproductive) as the G-type plants but in the case of the G2-type plants the proportion of reproductive nodes is much greater (Figs. 3 and 4).

Interrelationships among the four response types and the mode of inheritance are being studied, but for purposes of illus-

TABLE 1. Mean number of reproductive nodes and grams of dry seed per plant in parental, F_2, and F_3 populations cultivated under natural short days in the greenhouse (1966). Cross between two photo-insensitive parents produced a photo-sensitive F_1 and segregating F_2 and F_3 populations

Population	Response class	No. reproductive nodes	Gms. dry seed per plant	Number of plants
P_1	I	5.5	3.5	15
P_2	I	3.0	1.4	15
F_2	I segregants	4.2	2.8	35
	G_2 segregants	49.5	29.1	44
F_3	I segregants	4.7	2.6	65
	G_2 segregants	49.5	28.5	39

Fig. 3. Three photo-dependent response types in peas. Left (G2-type): reproductive phase is initiated early, but apical growth continues despite irregular production of fruits and seeds. Note presence of flowers at apex and fully mature fruits near base. Center (K-type): flower initiation is delayed but, once begun, normal reproductive activities lead to rapid senescence and plant death. Right (G-type): flowering is inhibited; plant remains vegetative. All plants grown under short day conditions.

Fig. 4. Schematic representation of two actual F_2 segregants cultivated under SD conditions. Left: a photo-sensitive (G2-type response) plant, and right, an insensitive plant. Under LD both plants would behave as plant at right. Nodes below dashed line are vegetative; those above are reproductive. Note intermittent occurrence of aborted reproductive nodes (solid diamonds).

trating the effects of the genotype and the environment upon senescence the results of only one cross are presented here.

Crosses between G-type and I-type plants produce all four response classes in F_2 if the populations are cultivated under SD conditions. Selected insensitive derivatives from such crosses, when themselves outcrossed to another insensitive inbred line (I x I), have given rise to G2-type plants in F_1. In F_2 both insensitive and responsive segregants appeared (Table 1). Two criteria of response, viz. the number of reproductive nodes and the weight of the dry seed per plant, show a tenfold
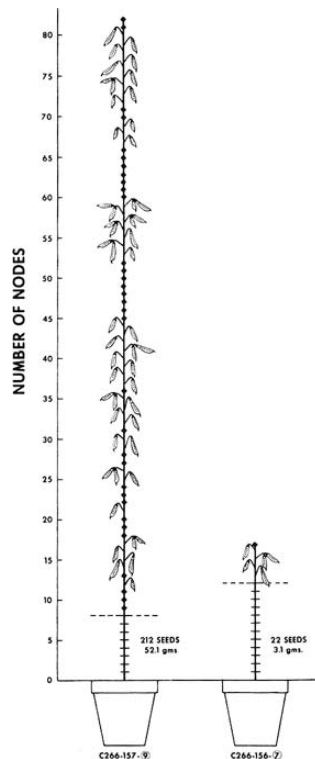
increase in favor of the responsive segregants. In this relatively small population, the ratio of responsive to insensitive plants was 44:35 (a perfect fit to the theoretical 9:7 dihybrid ratio). An earlier experiment gave an observed ratio of 29 responsive to 30 insensitive. Presumably, then, dominant alleles at two different loci are necessary to evoke a response under SD.

These data reveal that plants with the appropriate genotype cultivated in an appropriate environment will continue to grow for a prolonged period of time despite the production of fruits and seeds. This is further evidence that reproductive development and senescence are not causally related. Moreover, these results are

interpreted as indicating that, at least in certain genotypes of Pisum cultivated under specific conditions, vegetative development is independent of reproductive development.

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