植物之老化

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老化(senescence)是植物在生長過程中所表現的一種生理現象，因植物種類及器官的不同而有迥異的表現。在低等單細胞植物如細菌，因爲可經由細胞分裂直接繁殖，所以老化現象不明顯，只有在環境不良時，可形成厚膜來保護，並呈現生長停頓狀態。高等植物中，以種子來延續生命的一生只開花一次(monocarpic)的草本植物，在開花後即開始老化，使得葉片中之同化物得以轉流至種子，促使種子充實而傳宗接代，因此開花被認爲是老化的訊號，而種子則扮演強勢的積儲(sink)。依靠貯藏性器官來越過不良環境的植物如馬鈴薯，塊莖爲強勢積儲，使葉片(供源，source)中之同化物轉流至塊莖。多年生木本植物如樹木類，在遭逢逆境如乾旱或低溫時，均經由老化過程來回收同化物，以增加對逆境的忍受性，因此，如逆境來得突然，植物來不及應變時，即有可能死亡。

高等植物的老化，至少包含葉片、花、果實等，老化的生理變化，重要的包括細胞構成分之分解，用以再利用並輸送至種子或果實，總蛋白質減少(水解後送出)、核酸減少、RNA及DNA仍有高活性，新水解每活性增加、葉片老化之初期質體降解、葉綠素含量減少、光合速率降低、呼吸作用與粒線體維持正常等。有關老化之假說，有老化因子論、營養流出論、營養再分配論等，爲了這些研究，經常被利用之設計有摘花、摘果及環狀剝皮試驗等，如雄波菜摘花後可延緩老化，用以證明開花因子論；波菜抽苔不開花就不老化，用以證明非營養流出論等；禾本科植物以熱環剝(heat girdling)配合放射性元素之偵測來瞭解同化物之走向等。這些單一的老化理論並未能解釋所有的老化現象，但老化受外在因子如溫度或水分之影響仍無可置疑的。植物荷爾蒙中，細胞分裂素(cytokinins)對於離體葉片之老化有抑制作用，影響根形成細胞分裂素的因素如淹水、缺水及斷根等均會引起葉片老化，引起膜質過氧化作用(lipid peroxidation)的自由基(free redicals)及lipoxygenase活性受細胞分裂素抑制，細胞分裂素也增加Ca的濃度；乙烯促進葉片老化；離層酸(ABA)大抵上促進老化；生長素(auxin)與老化之關不明確；GA對於葉片中葉綠素含量之影響不明確；茉莉花精(jasmonates)促進葉片老化與塊根之形成。

植物之老化現象可利用於景觀佈置、風景區之規劃、禾穀類增產(如小麥收穫前噴施尿素液於葉面以造成老化)、及果樹產量與果實品質之提升等。

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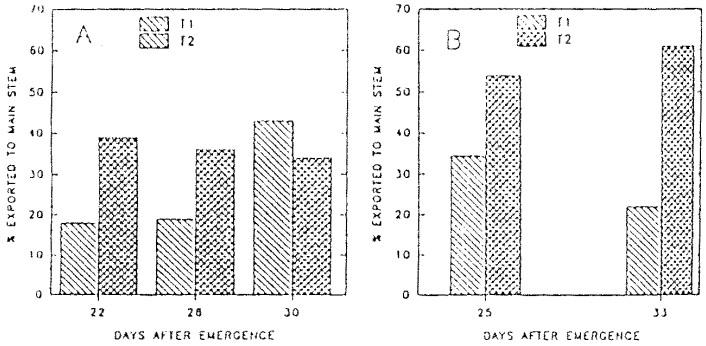

Figure 8.6. Portion of current photoassimilate (from $^{14}CO_2$ labeling) exported from tillers of barley to the main stem in chases where A) both tillers survived and B) T1 survived, while T2 did not. The nonsurviving tiller exported much of its ^{14}C to the main stem (data from Lauer and Simmons, 1988).

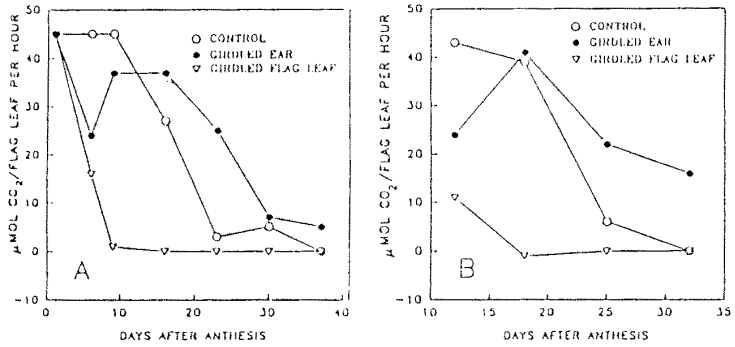

Figure 8.5. Total photosynthesis (net photosynthesis + dark respiration) of flag leaf of wheat, steam girdled below the ear, or steam girdled at the base of the flag leaf. Girdling took place either A) 1 day after anthesis or B) 10 days after anthesis. Removal of the ability of the ear, the primary sink, to import results in a delay in the decline of photosynthesis, while preventing the flag leaf from exporting leads to a very rapid cessation of photosynthesis (data from Frohlich and Feller 1991).

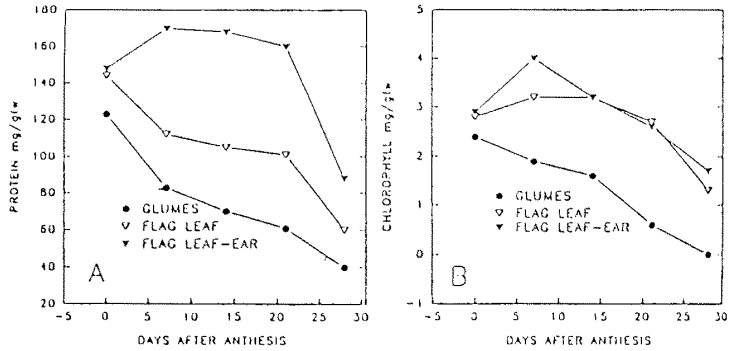

Figure 8.4. Senescence of flag leaf and glumes in wheat, measured by A) protein and B) chlorophyll content. Deheading (flag leaf ≈ ear) resulted in a delay of protein loss, and a slight slowing of the decline of chlorophyll in the leaves. The glumes, though developmentally younger, show a more rapid loss of protein and chlorophyll than the flag leaf (data from Biswas and Mandal 1986).

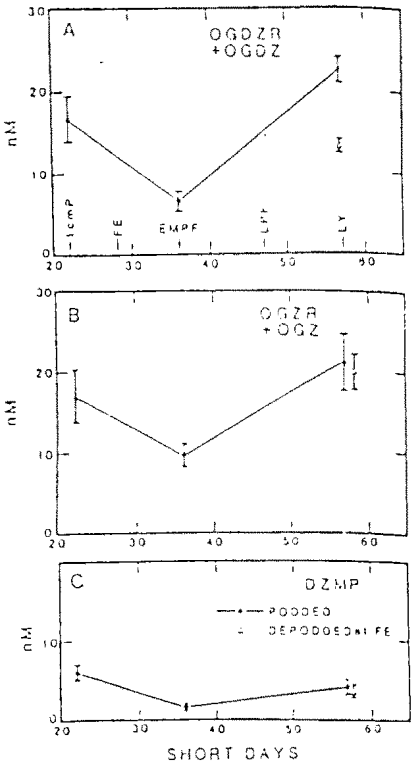

Figure 5. Changes in the xylem sap concentrations of (A) OGDZR + OGDZ, (B) OGZR + OGZ, and (C) DZMP during pod development and monocarpic senescence and the ellects of depodding. Abbreviations and other details as in Figure 1.

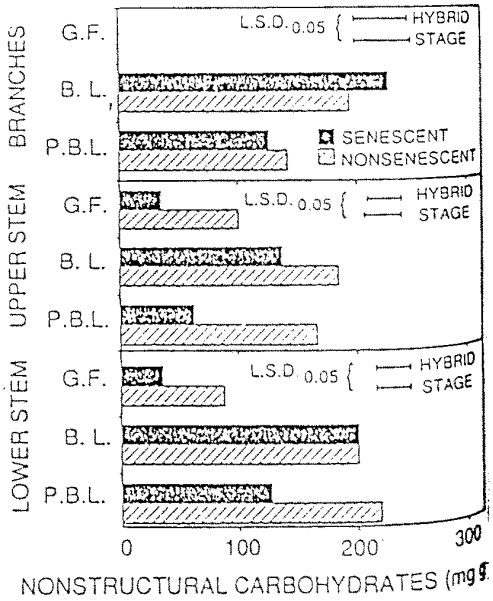

Fig. 1 Concentration of nonstructaral carbohydrates in branches and lower and upper stem of senescent (Atx378×RTx7000), and nonsenescent (Atx623×RTx5388) hybrids of sorghum averaged over 1982 and 1983. The parts were sampled 5 or 7 d after pulse-labeling (^{14}C) of plants during grain filling (GF) and at black layer formation (BL) and post-balck layer formation in grain (PBL).

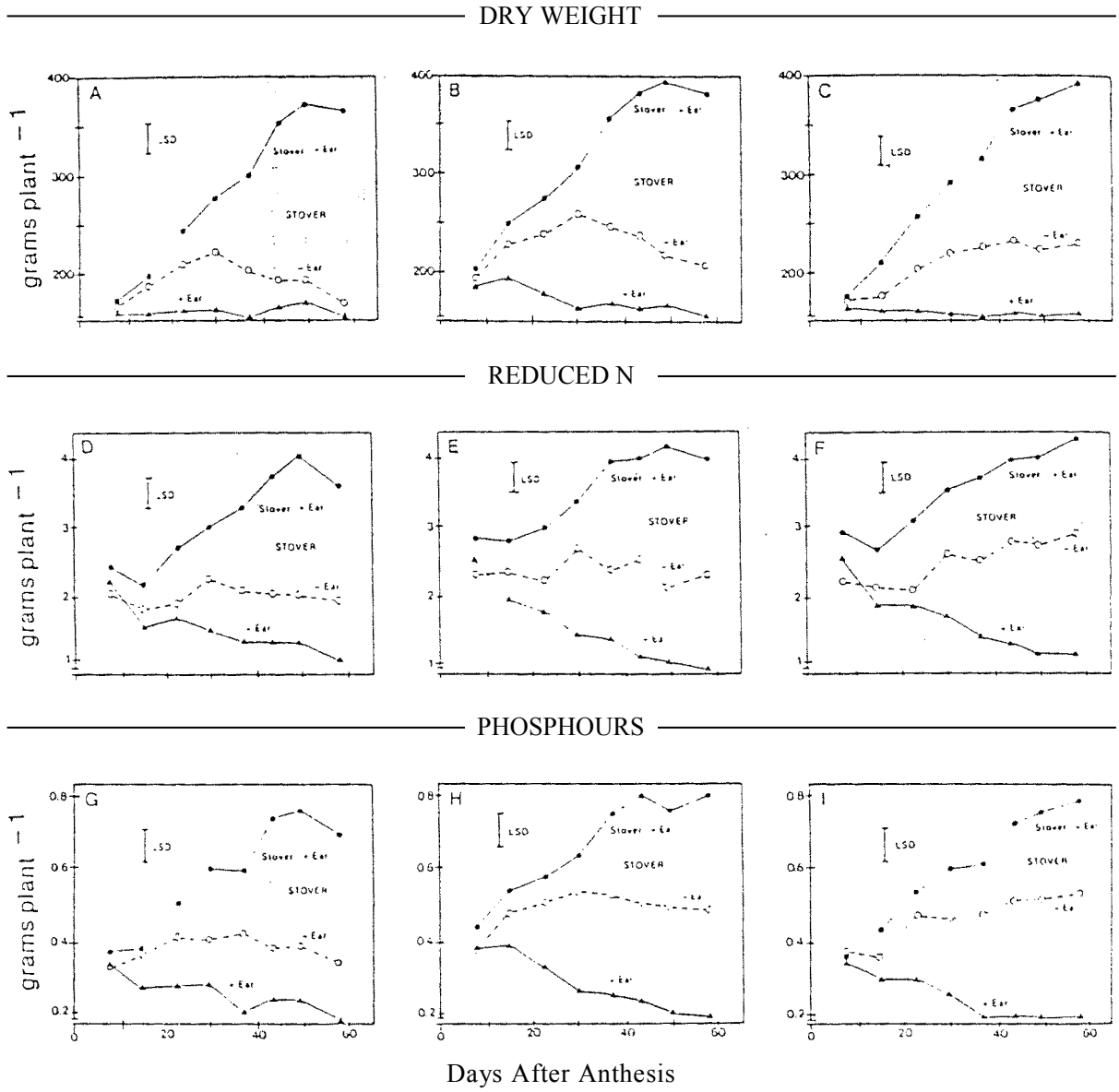

Fig. 1. Effect of ear removal on dry weight and constituent content of whole plants (above ground portion) of three maize hybrids. Treatments involved bagging and excising the primary car shoot and any secondary ear shoots (–ear) compared with controls (+ear) which were intact plants including all above ground parts except husk and tassle. The curves designated stover + car represent data for stover + grain of the control treatment. Curves under the subheading STOVER represent data for the stove fraction only of earless (–ear) and control (+ear) treatments. The LSDS shown are applicable between treatments within time, and within treatments across time. Grain yield at maturity was 185, 208, and 199 g plant^{-1} for P3382, B75×Mol7. and FS854, respectively.

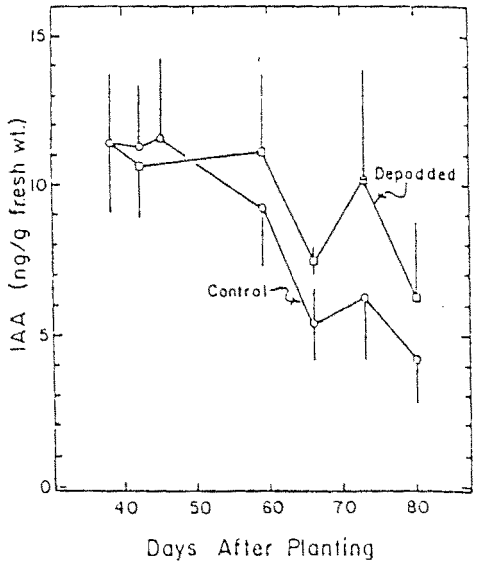

Fig. 2. Concentrations of IAA in second most recently expanded infoliolate leaf. The depodding treatment consisted of removing all reproductive tissue 32 h before exudate collection. Values represent means of six replicates and their SE.

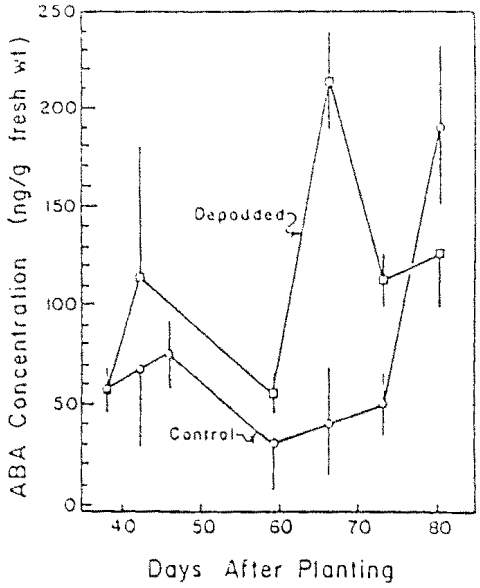

Fig. 1. Concentrations of ABA in second most recently expanded trifoliolate leaf. The depodding treatment consisted of removing all reproductive tissue 32 h before exudate collection. Values represent means of six replicates and their SE.

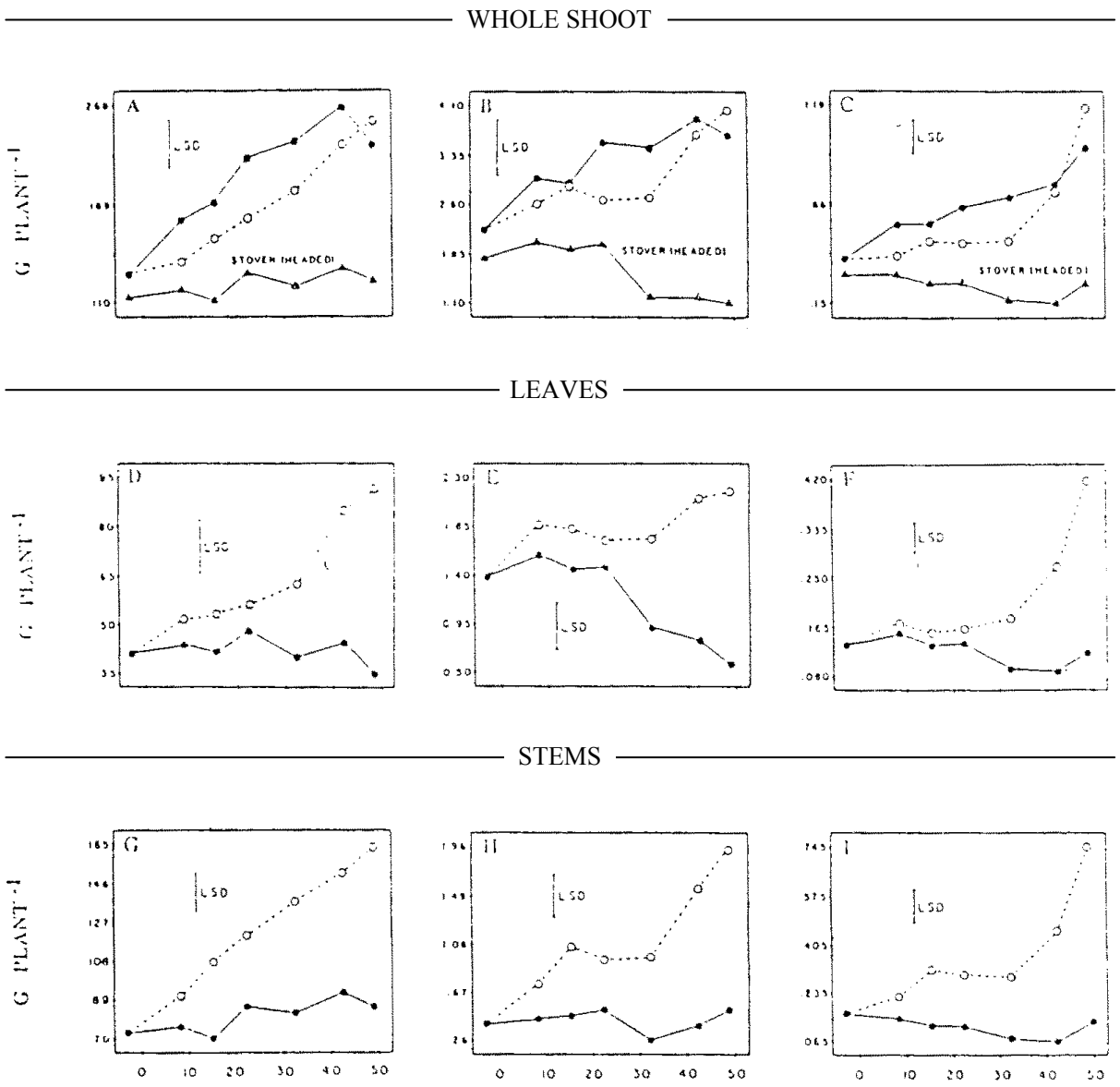

Figure 1. Effect of seedhead removal from sunflower on dry weight and constituent contents of whole shoots (above ground portions), leaves, and stems during the seed tilling. (○---○), deheaded plants, (●---●), control plants with intact seedheads. Curves designated STOVER (▲---▲) represent data for the vegetative (leaves plus stems) fraction only of control plants. The LSDs shown on the figures are applicable belween treatments within time and within treatments across time.

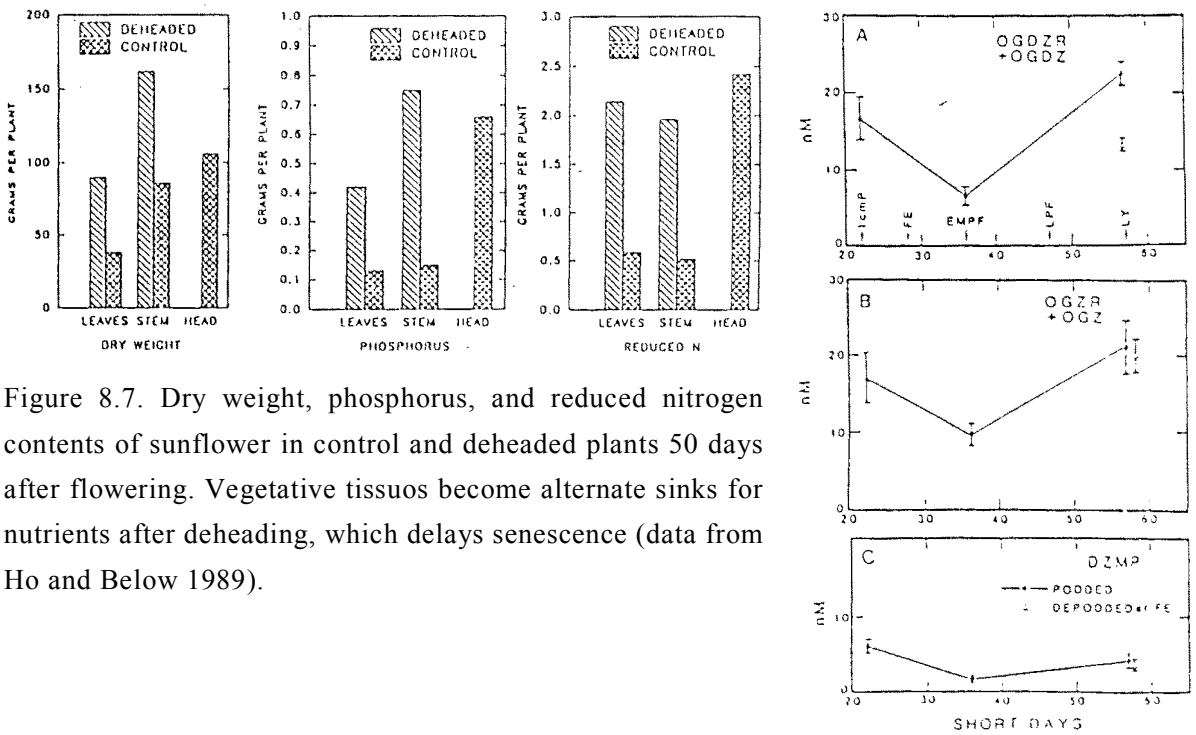

Figure 8.7. Dry weight, phosphorus, and reduced nitrogen contents of sunflower in control and deheaded plants 50 days after flowering. Vegetative tissuos become alternate sinks for nutrients after deheading, which delays senescence (data from Ho and Below 1989).

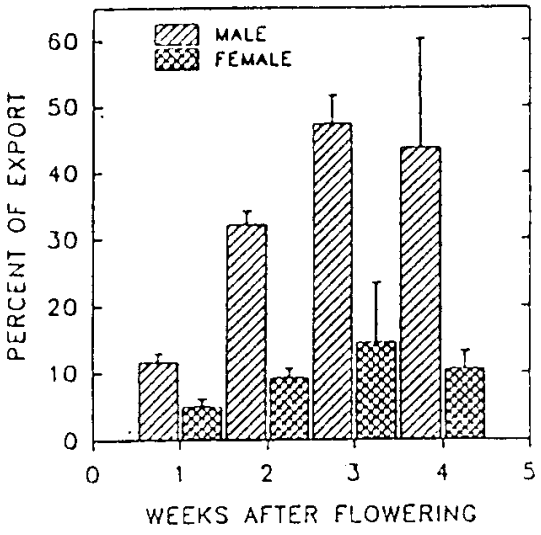

Figure 8.15. Allocation of radioactivity to reproductive structures is compared in spinach plantes at ages ranging from 1 to 4 weeks after flowering. The plants were labeled with radioactive $^{14}CO_2$ at the leaf immediately below the inflorescence. The males show a substantially higher allocation to the reproductive structures during this time (Sklensky and Davies, unpublished data).

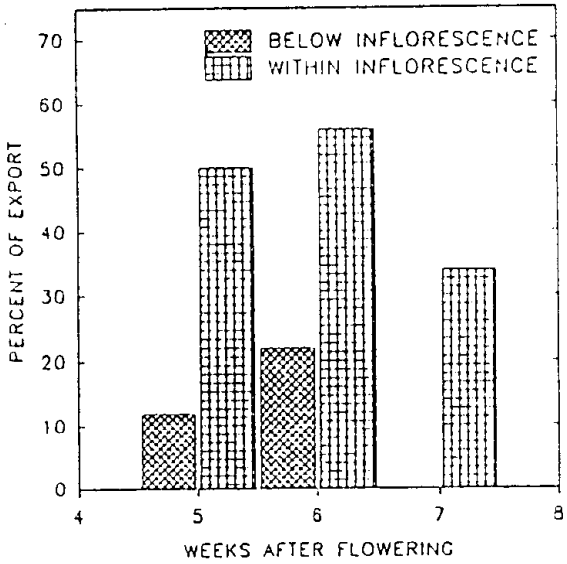

Figure 8.16. Allocation of radioactivity to the fruits of female spinach plants from various treated leaves. The leaf just below the inflorescence provides little of its exported radioactivity to the reproductive organs, while leaves within the inflorescence provide a much higher percentage of their export to the flowers and fruits (Sklensky and Davies, unpublished data).

Figure 8.12. Apical portion of G2 pea in long days. Flower buds expand rapidly, to the extent of emerging from the apical bud (from Kelly and Davies 1986).

Fig. 8.13. Apical portion of G2 pea in short days. Floral development is slow, with a small closed flower bud, and an open flower

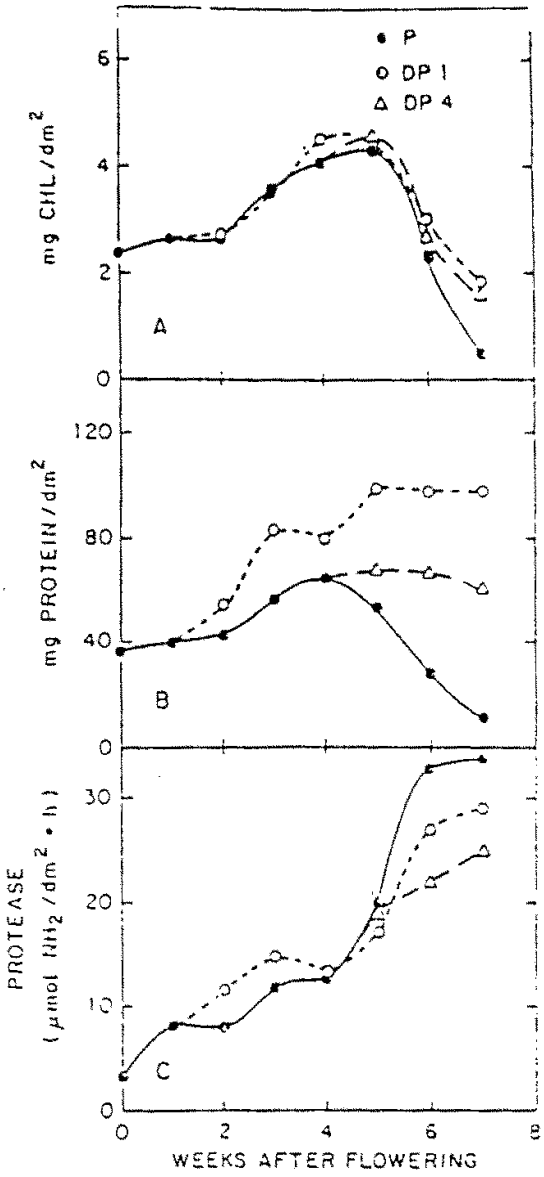

Fig. 2. Changes in Ch1 (A). protein (B). and protedlyuc (C) activity of leaves from control. podded (P. •) plants, and plants continuously depodded beginning 1 week (DP1. ○) or 4 weeks (DP4. △) after flowering. The SD for CH1 ranged from ± 0.13 to 0.24 mg/dm^2; for protein, from ± 5.7 to 9.6 mg/dm^2; and for protease, form ± 1.8 to 4.9 μmol NH_2/dm^2·h.

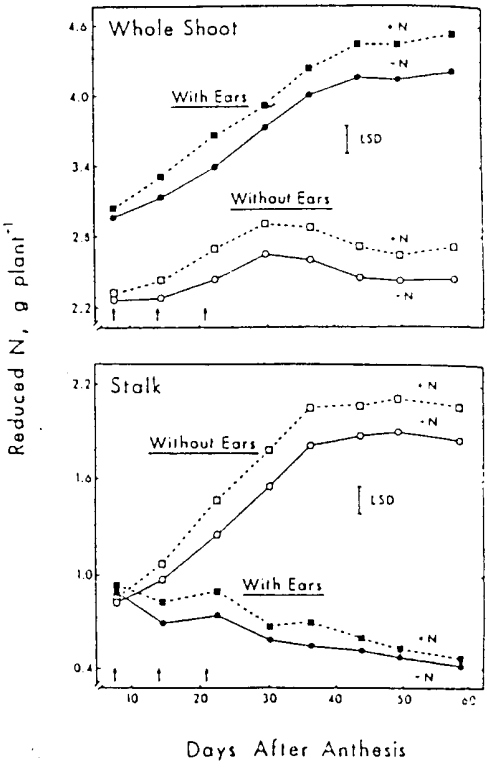

Fig. 1. Effect of foliar N application to eared and earles maize plants (cv B73 × Mo17) on the changes in reduced-N content of the whole shoot (A) and stalks (including lear sheaths) (B) during the grainfilling period. Arrows indicate time of N applications. Other details are in Table 1.

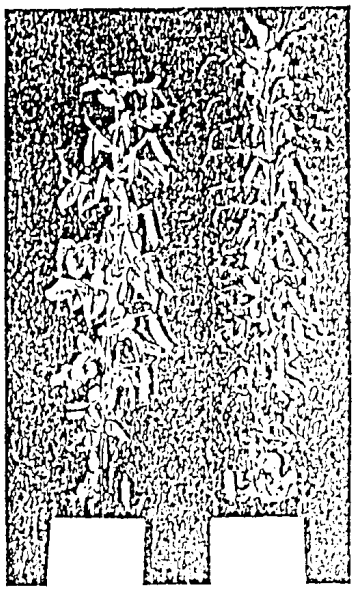

Figure 8.11. G2 peas grown in long days and short days (at different photon flux densities to control for photosynthesis effects of day length). The long-day plant on the left is showing signs of senescence, while the short-day plant continues vigorous flowering, fruiting, and

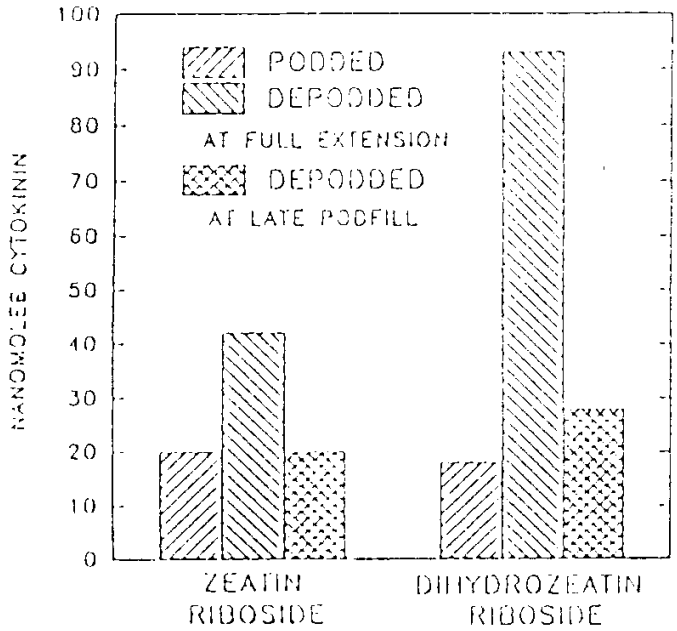

Figure 8.10. Depodding of soybeans at full extension of pods leads to an increase in dihydrozeatin riboside (DZR) and zeation riboside (ZR) in the leaves, and decreases leaf senescence, while depedding at late pod fill has no effect on senescence and little effoct on DZR or ZR (data from Nooden at al. 1990).

Figure 8.2. The separation of bolting and flowering effects on senescence in spinach plants. From left to right: 1) short days, 2) short days + gibberellic acid, 3) long days, 4) long days + gibborellic acid. Bolting alone does not produce senescence; some factor involving the production of the small male flowers induces senescence (from Janick and Leopole. 1961).

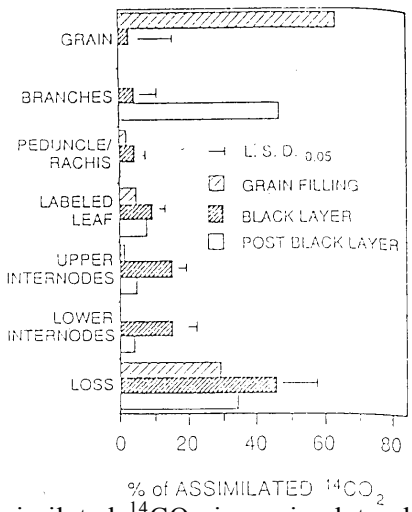

Fig. 3. Mean pereentages of assimilated $^{14}CO_2$ in grain, lateral branches, peduncle and rachis, labeled penultimate leaf, and upper and lower internodes at 5 and 7 d after pulse-labeling in 1982 and 1983, respectively. Plants were exposed to $^{14}CO_2$ during grain filling. at black layer and post black layer of grain. Percentages are averaged over two years and hybrids. Lines drawn to right of bars represent least significant difference [LSD (0.05)] for mean separation among stages for each part.

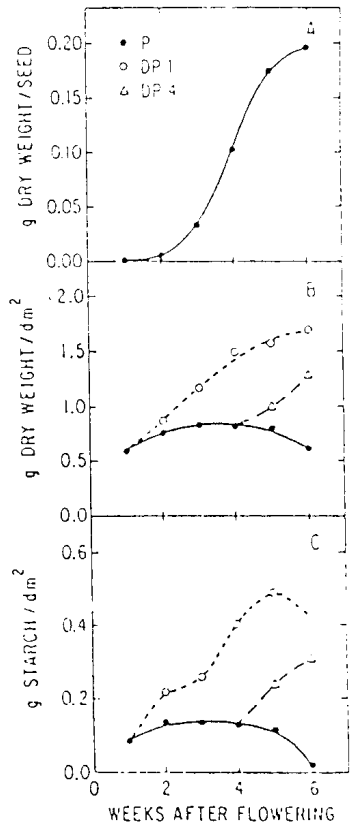

FiG. 6. Seed development in control, podded plants (A). and changes in specific leat weight (B) and starch content (C) of leaves from podded (P. •) plants and plants depedded beginning 1 week (DP1. ○) or 4 weeks (DP4. △) after flowering.

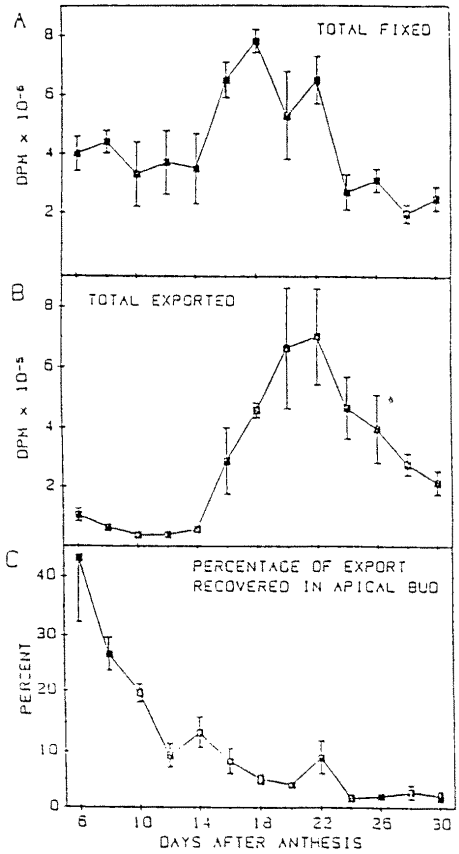

FiG. 4. Time course of total tion (A). total export (B). and percent exported to the apical bud (C). in pea plants grown in LD. as a function of the age of the treated pod. Pods were treated with $^{14}CO_2$ for 6 h and the plants harvested after 48 h.

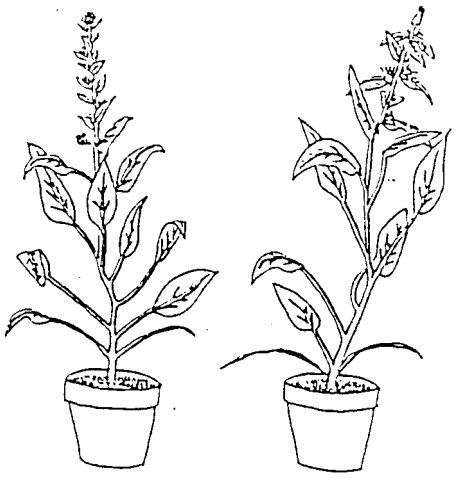

Figure 8.14. Male (left) and fernale (right) spinach plants of a rapidly bolting variety XPII 1510 in long days. The male plant has much smaller leaves in the inflorescence than the female. While male inflorescences are small, female flowers are even more inconspicuous until fruit formation is advanced.

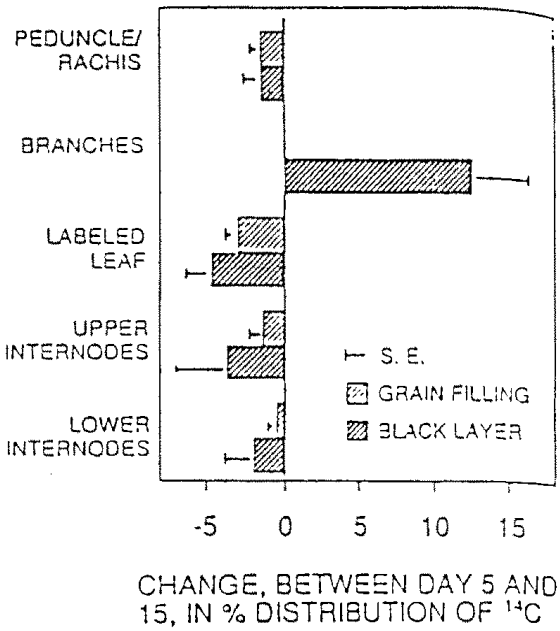

Fig. 4. Changes of percentage of assimilated $^{14}CO_2$, averaged over hybrids. in peduncle and rachis. lateral branches. labeled penultimate leaf. and upper and lower internodes between 5 and 15 d after exposure of penultimate leaf to $^{14}CO_2$ in 1982. Leaves were exposed during grain filling and at black layer. For each part plotted on the graph. the percentage of assimilated $^{14}CO_2$ was significantly ($P \leq 0.05$) different between the 5 and 15-d chase periods.