

STUDIES ON *Acaena* (ROSACEAE):
II. LEAF PRODUCTION AND SENESCENCE IN
Acaena magellanica (Lam.) Vahl

By D. W. H. WALTON

ABSTRACT. In favourable sites, vegetative shoots can produce up to 16 leaves during summer. The overwintering terminal bud is protected by the last three leaves produced in the previous season. Peak shoot photosynthetic efficiency is reached in January and by mid-February leaf mortality exceeds natality. Although effectively deciduous, true abscission does not occur, leaflets mainly decaying quite quickly *in situ*, although petioles may persist on the stem for several years. This leaf cycle is contrasted with those of other species.

STUDIES on dry-matter production in adult plants of *A. magellanica* on South Georgia have been published by Walton (1973, 1976). The numbers of leaves produced by current-year shoots at various sites was discussed (Walton, 1976) and found to be less in sites with short growing seasons. Leaf size has also been shown to be highly variable in this species (Walton and Greene, 1971). A simulation model of dry-matter production in a mature *A. magellanica* community on South Georgia (Jones and Gore, in press) showed a very high annual turn-over of biomass, nearly all of which was attributable to the leaves. Although the species appears to be deciduous, in that most leaves are lost before the beginning of winter, the leaves are not shed as in most deciduous species; they remain attached to the stem whilst the lamina decays *in situ*. The petioles themselves may remain on the stem and take several years to decay.

The considerable proportion of dry matter involved in the annual production of leaves, together with the highly plastic response of leaf growth to competition and local environment made it essential to conduct a more detailed study on a single shoot basis of leaf production and decomposition, so that data gathered on a community scale could be more easily interpreted.

METHODS

A south-facing community of *Acaena magellanica* with an understorey of *Tortula robusta* Hook. et Grev. growing on a dry scree slope was selected for the study. This site (Shackleton) has been described by Walton (1977). The community was a mature stand with a leaf-area index of over 4 in mid-season. Current-year terminal shoots were harvested at intervals throughout the 1973-74 summer, with groups of ten random shoots being used for pigment and dry-matter analyses. Successive leaves were removed from each shoot in order of age and bulked to give a sample of ten leaves for each age class. These were analysed for chlorophyll content after homogenization in 80 per cent Analar acetone with $MgCO_3$ added to prevent acetolysis of pigments. Absorption of the extracts was read at 750, 663, 652 and 645 nm. on a Unicam SP 600 spectrophotometer (Sestak, 1971) and chlorophyll content calculated using Arnon's (1949) formulae. For weight and area analysis, further samples of leaves were removed from the shoots in the same manner. The fresh weight of each leaf was determined and its area measured before drying at 70°C and re-weighing. Leaf-area measurements were made on an airflow planimeter (Jenkins, 1959).

Measurements were made of the length of stem for each sample and notes made on the appearance of each leaf age class at each harvest. From the fresh weight/dry weight ratios, chlorophyll content was adjusted to a mg./g. dry-weight basis. Summation of mean leaf area and mean dry weight for each age class provided leaf area and dry weight per shoot data for each harvest. This method of sampling allowed the rate of leaf decomposition to be studied whilst the leaf was still attached to the shoot.

RESULTS

The seasonal changes, on a per shoot basis, in number of leaves, total dry weight, total chlorophyll and leaf area are shown in Fig. 1. The pattern of growth was as follows: the peak

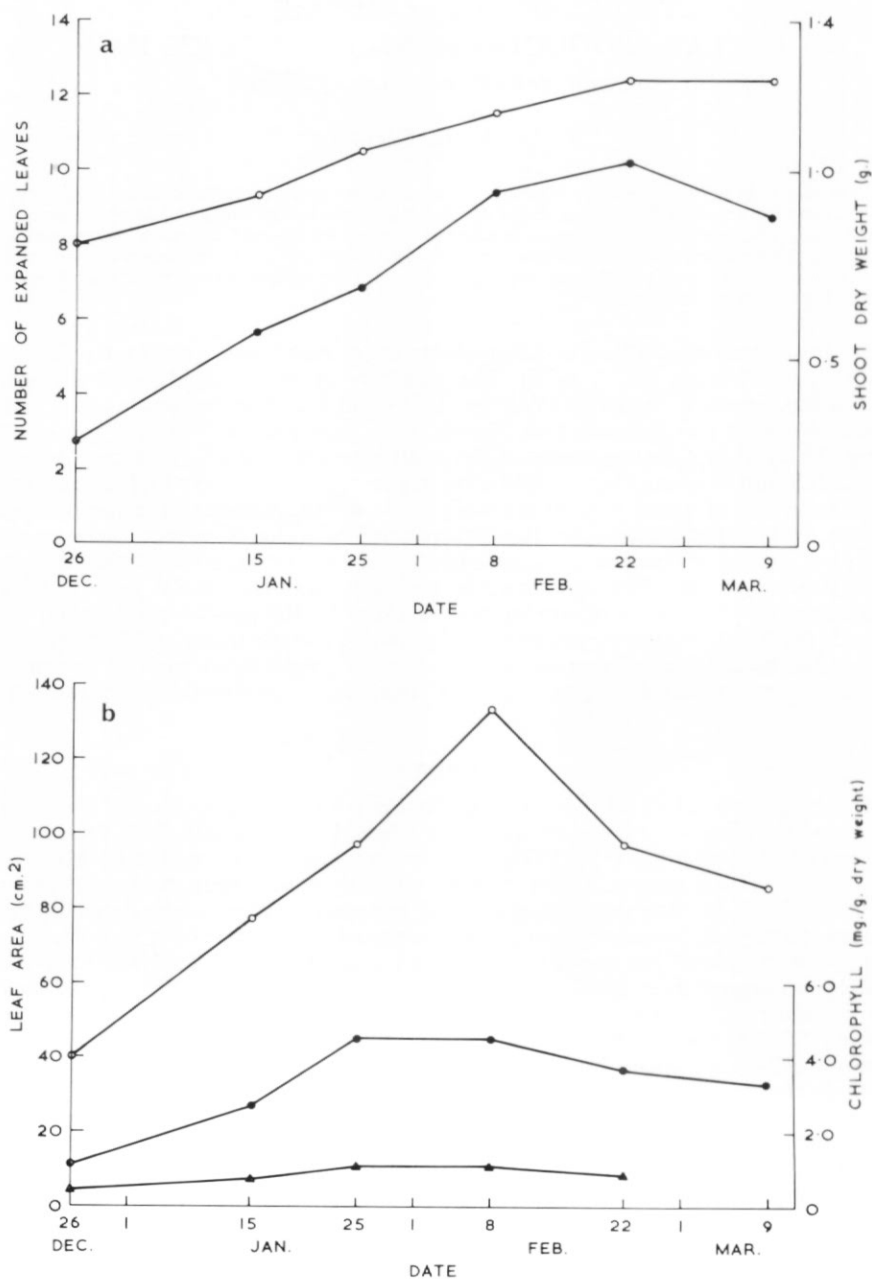


Fig. 1. Growth data for the total shoot.
 a. Shoot dry weight (●) and number of expanded leaves (○).
 b. Leaf area (○), total chlorophyll (●) and chlorophyll b content (▲).

chlorophyll level was achieved in late January, with leaf expansion continuing until a maximum leaf area was reached in early February; towards the end of February leaf production ceased, a mean leaf number of just over 12 expanded leaves having been reached, and shoot dry weight then began to decline. This overall pattern was investigated in more detail to discover how the pattern of leaf production and growth changed during the season on an individual shoot.

Since much of the decay of leaves in this species takes place whilst the leaf is still attached to the plant, the normal methods of studying decomposition, such as litter bags, cannot realistically be used. The death of the leaf is primarily the death and disintegration of the lamina, the petiole often persisting over several seasons attached to the shoot. The characteristic course of leaf death is the gradual yellowing of the leaflets which eventually turn brown and dry up. They are then usually removed from the petiole by the action of wind, rain and snow, to finally disintegrate on the ground. Leaf death can be measured in at least four ways: namely, a decline in chlorophyll content, leaf area, fresh weight and dry weight. The onset of death is perhaps best measured by change in pigment content, whilst the later stages of loss of leaflets and the drying of the lamina can be conveniently studied by changes in leaf area and weight, respectively.

To establish the typical relationship between leaf number, leaf size and rhizome length at the site, a leaf spectrum is presented in Fig. 2. Maximum leaf size was achieved by leaves 9 and

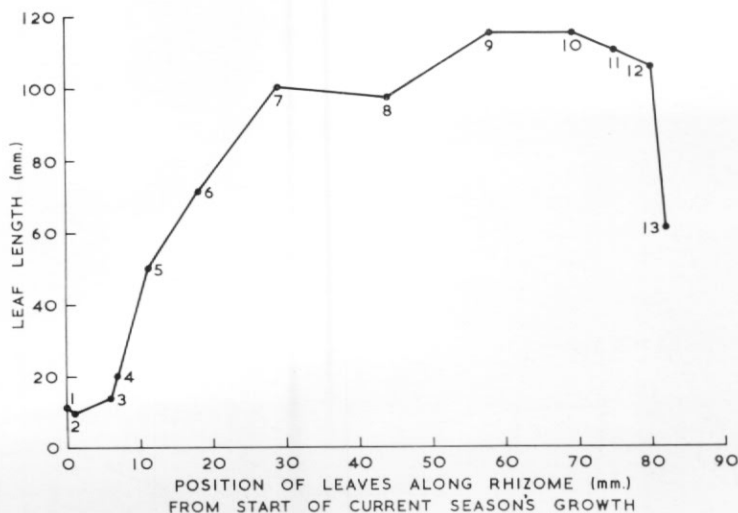


Fig. 2. Leaf spectrum for a typical current-year shoot in late January.

10, whilst the length of the internodes suggested that shoot growth was at its most active during the period between leaves 6 to 10. Although only 13 leaves are shown, two further differentiated but unexpanded leaves were also present.

In a living leaf the ratio of dry weight/fresh weight is usually *c.* 0.2. During senescence the plant withdraws as much useful material as possible and the leaf shrivels. The biological change in water content causes a change in the ratio which increases to almost 1.0. After the leaf has passed the point of death, the ratio falls again due to the physical uptake of water by the dry tissues. This ratio can serve as an indicator of the stage of senescence reached. Chlorophyll content often begins to decline before a change in leaf-water content can be detected and is normally the earliest indicator of senescence.

Although harvesting was started rather late in the summer (26 December 1973), it was still possible to follow the patterns of growth and death of most of the leaves on the shoot. The changes in chlorophyll content, leaf area, dry weight and fresh weight of each leaf during the growing season are shown in Fig. 3. The patterns for individual leaves are different in several

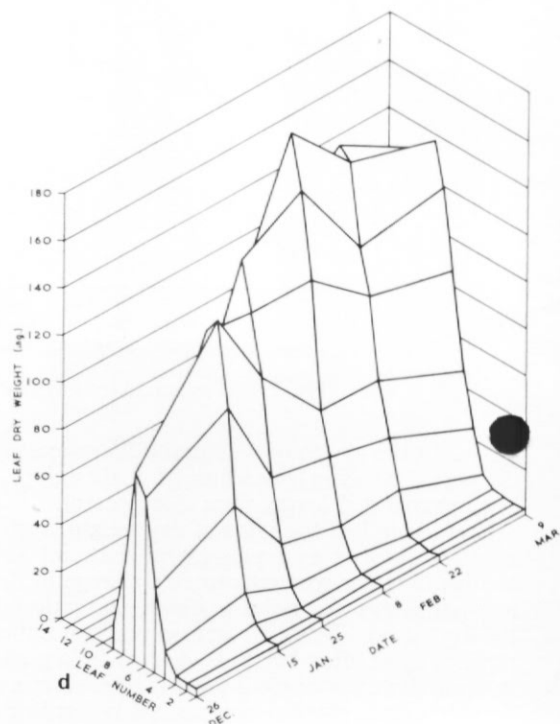
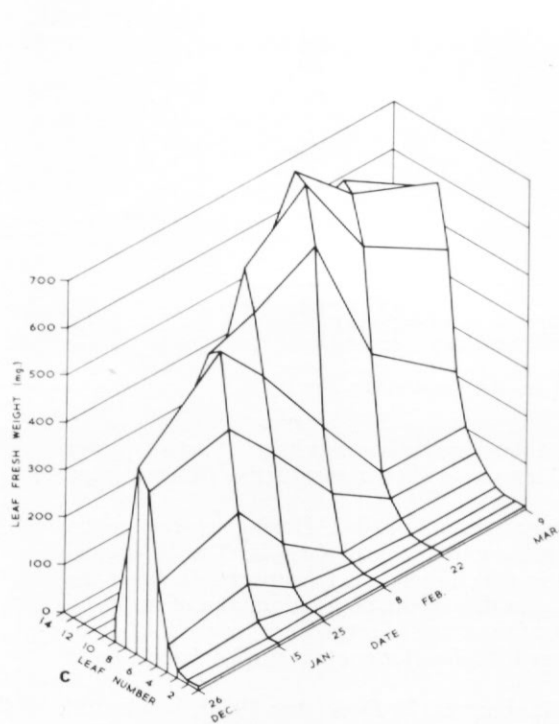
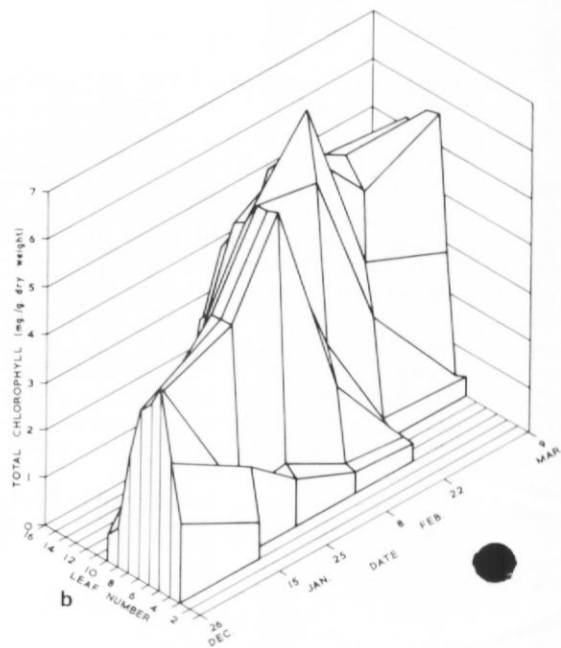
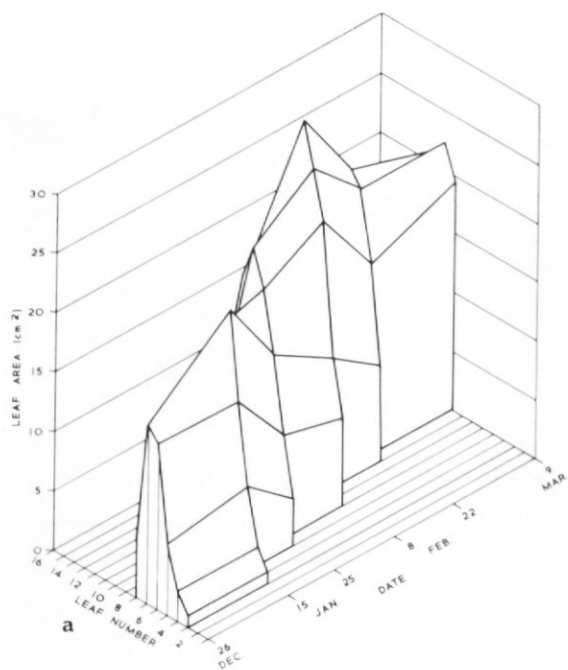


Fig. 3. Growth data for individual leaves.

- a. Leaf area.
- b. Leaf total chlorophyll (a+b).
- c. Leaf fresh weight.
- d. Leaf dry weight.

respects to the overall pattern shown by the whole shoot. In the early leaves, dry weight begins to decline before chlorophyll reaches its peak, the reverse of the whole shoot pattern (Fig. 1). However, in leaf 8 dry weight and chlorophyll reach their peak together, whilst in the later leaves chlorophyll declines before maximum dry weight is reached.

There is a correlation between leaf length, leaf area and fresh weight. Leaf 10 is the largest and heaviest, and appears to have been differentiated at the end of December and to have reached its peak area and pigment content in early February, a little before maximum fresh weight. During the course of the summer up to 15 leaves were produced on the vegetative shoots and from notes made at harvest some inferences can be drawn about leaf initiation.

At the first harvest in late December, leaf 1 contained no chlorophyll and leaves 2 and 3 were brown, probably due to pigment destruction during the winter. These first three leaves, although apparently normally differentiated, never expand properly. The majority of their pigment is in the petiole and stipules. They are overwintering leaves, differentiated at the end of the previous season, and act as bud scales for the shoot apex during the winter. It is not certain whether leaf 4 is also formed the previous season. In leaves 4 and 5 the leaflets unfold normally but the leaves are small and often the petiole does not expand to its usual length, causing a "bunching" of leaflets. If leaves 4 and 5 are treated as the first leaves of the new season, it seems likely that their aberrant development may be due to the severe frosts common during the immediate post-melt period. Leaf initiation is assumed to start at or slightly before snow melt (mid-October onwards depending on site) and up to 16 leaves can normally be produced by a shoot. Production ceases in late February, the shoot having reached maximum efficiency during January. Fig. 4 shows the probable pattern of leaf production during a year.

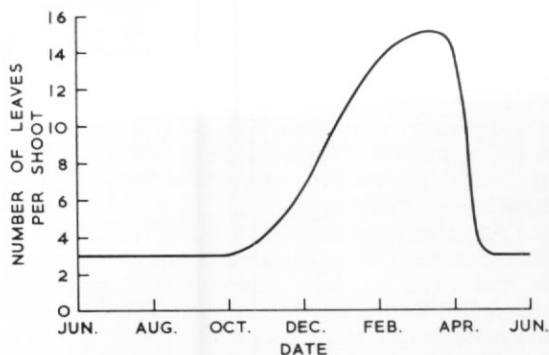


Fig. 4. Suggested pattern of production in the annual leaf cycle of a shoot.

In mature communities of *A. magellanica*, leaf decay is hastened by self-shading and the humid micro-climate maintained within the canopy. Fig. 4 shows a sharp decline in leaf number during late March–early April but at the beginning of March leaves 1 to 8, although still attached to the shoot, are effectively dead in terms of ability to photosynthesize. If the decline in chlorophyll content is taken as the onset of leaf death, leaves approaching or having reached peak pigment content can be termed the photosynthetically "effective" leaves. This can also be applied to leaf area. Fig. 5 illustrates the changes in "effective" number of leaves and leaf area per shoot and shows that leaf death exceeds initiation at the end of January. "Effective" leaf area continues to rise until early February due to the rapid expansion of the large leaves 10, 11 and 12, after which a rapid decline ensues.

True abscission does not occur, leaflets decaying whilst attached to the petiole. Attack by a fungus, *Ovularia* sp. (personal communication from R. Watling), growing on the leaves is characteristic of all plants of *A. magellanica* on South Georgia. The first yellow marks appear on the oldest leaves during late January or early February. It normally appears first in north-facing stands and spreads most quickly in closed communities. Examination of herbarium material suggests that it occurs throughout the range of this species. By early March all except the unexpanded leaves are infected. Field observations have suggested that the fungus is

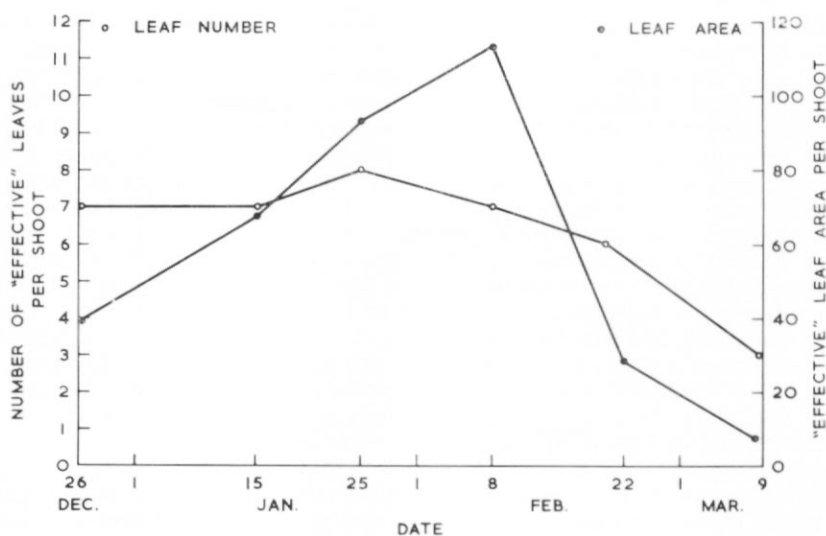


Fig. 5. Changes in numbers of "effective" leaves and in "effective" leaf area per shoot during the growing season ("effective" is total present minus dying).

saprophytic on the senescing leaves and may serve to considerably hasten their decay. It has also been found on leaves of the hybrid, *A. magellanica* × *A. tenera*. Hennings (1906) recorded five species of fungi (*Sphaerella acaenae* P. Henn., *Physalospora acaenae* P. Henn., *Pleospora acaenae* P. Henn., *Phoma acaenae* P. Henn. and *Staganospora acaenae* P. Henn.) as occurring on *A. magellanica* leaves and stems from Iles Kerguelen. Nothing is known of the ecology and distribution of these fungi in the sub-Antarctic but it is possible that some may also be present on South Georgia as active agents of decomposition.

Despite the limitations previously mentioned in using the litter-bag techniques to assess decomposition in this species, some preliminary data of this type have been collected. The rates of loss of dry matter from mature leaves placed in nylon mesh bags were very high, over 90 per cent disappearing in under 2 months during the summer. The last parts to disappear were the petioles. The fact that the petioles did disappear, whilst in normal circumstances they would have remained attached to the stem for possibly several years, shows clearly that losses from litter bags cannot be assumed as necessarily comparable with natural decomposition. However, the pattern of leaflet loss followed by slower petiole disintegration was similar in both studies. Anatomical examination of the petioles (author's unpublished data) has shown that considerable accumulations of crystals are common and this may be important in delaying tissue break-down. Litter in bags placed within *A. magellanica* stands disappeared much more quickly than in bags placed in *Festuca contracta* grassland. The humid micro-climate maintained within the dwarf-shrub canopy is clearly of great importance for decomposition.

Walton (1976) has shown that the flowering shoots in *A. magellanica* have only six or seven leaves. Since these shoots are always terminal and assuming the number of overwintering leaves is the same as for the vegetative shoots, i.e. two or three, floral initiation must occur after initiation of three leaves in spring. This would allow time for expansion of sufficient leaves on the flowering shoot to support at least part of the dry-matter requirements of floral development. Tracer experiments with ^{14}C have established that the majority of photosynthate produced in a flowering shoot is used by the capitulum (author's unpublished data).

DISCUSSION

In the context of the sub-Antarctic islands, *Acaena magellanica* is an important species from both biogeographical and ecological points of view. The large stands formed by this species

have high annual production rates (Walton, 1973), which make the study of its annual leaf cycle of considerable interest. The species is effectively deciduous although leaf abscission does not occur at the end of the growing season, and, since the break-down of the lamina material appears to be very rapid once it is removed from the petiole, the re-cycling of nutrients is likely to be quite quick in this community. This is in sharp contrast to the situation in the *Festuca contracta* T. Kirk grassland (Walton and others, 1975).

The cycle of leaf production and senescence in a mature lowland community on South Georgia appears to be as follows. The terminal meristem is protected over the winter period by the last two or, more usually, three leaves differentiated at the end of the previous summer. Leaf initiation commences at snow melt and continues until late February, by which time up to 16 leaves may have been produced. Of the overwintering leaves, only the third, i.e. the last one to be differentiated, grows appreciably during the second summer and this leaf together with leaves 4 and 5 appear to develop abnormally due to the effects of low temperatures or frosts in early spring. The largest leaves, 7, 8, 9 and 10, are probably initiated during December and expand to their maximum size during January-early February. This also appears to be the period for maximum growth of internodes. Of the various criteria for measuring leaf senescence, the change in chlorophyll content would appear to be the most sensitive, since translocation into a leaf may mask any weight changes due to the cessation of local dry-matter production. In terms of photosynthesis relative to leaf area, the shoot is at its maximum efficiency from early January until early February, after which the effective leaf area declines rapidly and leaf mortality exceeds leaf natality.

Shortly after the decline in total chlorophyll content the dry weight/fresh weight ratio begins to increase as the leaf dries up. The ratio usually reaches *c.* 0.8 (at which point the majority of the leaf cells have died), and then declines again as water is taken up solely by physical means. The drying out of the leaf results in reduction in leaf area and this continues as dead leaflets are removed from the lamina by wind, rain and snow. Break-down of the soft wet tissues is rapid once the leaflets are in the litter layer. The petioles persist, sometimes for several years, often with the petiole base remaining alive for storage purposes (author's unpublished data).

There has been little work in comparable detail on the leaf cycles of perennial species, although the fate of individual leaves and their importance to the plant has been extensively studied in various annual crop species. In a detailed study on *Nicotiana glauca* hort., Sestak and Catsky (1962) found that net photosynthetic rate decreased more rapidly than chlorophyll content in ageing leaves. They presented evidence showing increases in chlorophyll and photosynthetic rate during the early phase of leaf development up to "photosynthetic maturity". In *Nicotiana* it appears that leaves do not remain for long at their peak production rate, but this must vary with the rate of leaf production in any particular plant. The data in Fig. 3 suggest that, in *A. magellanica* leaves, size and weight also begin to decline shortly after reaching their respective peaks. If net photosynthetic rate follows a similar trend to that of *Nicotiana* the decline in "effective" leaf number and leaf area may be even sharper than supposed at present. Callaghan (1973) has studied the leaf cycle of *Phleum alpinum* L. on South Georgia and he believes that leaves of this species show maximum efficiency for only short periods. This high rate of leaf turn-over is in contrast to the low rates of leaf production and apparently long effective leaf life shown by evergreen Arctic shrubs such as *Cassiope tetragona* (L.) D. Don (Callaghan and Collins, in press) and *Dryas integrifolia* Vahl (Svoboda, 1972).

Although leaf size varies with position on the shoot, it also varies significantly between populations (Walton, 1976). It is a much more plastic character than leaf number. In mature stands, self-shading stimulates the production of larger leaves than are found on plants in pioneer communities. Field observations have suggested that leaf decay is slower on colonizing plants where the leaves do not form a closed canopy. In open habitats the leaves lie parallel to and close to the ground, are well separated on the shoot so that shading does not occur, and have a higher proportion of dry matter as lamina than is found in leaves from closed stands. This must allow greater leaf efficiency and must be a principal reason for the very large dry-matter increments of pioneer shoots (Walton, 1976).

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