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THE AUTECOLOGY OF SWEET BRIER
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SUBMITTED FOR THE DEGREE
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INTRODUCTION

Sweet brier is of particular interest in New Zealand, because it occurs widely as an unwanted plant in extensively grazed tussock grasslands of the eastern South Island. Since the control of the rabbit it has rapidly encroached on thousands of acres of pastoral land, causing much of it to become derelict, and forcing large tracts of land out of production.

In the past, control measures have been many and varied, with usually disappointing results. The difficulty and high cost of eradicating sweet brier in these areas have stimulated a desire for further research on this aggressive plant.

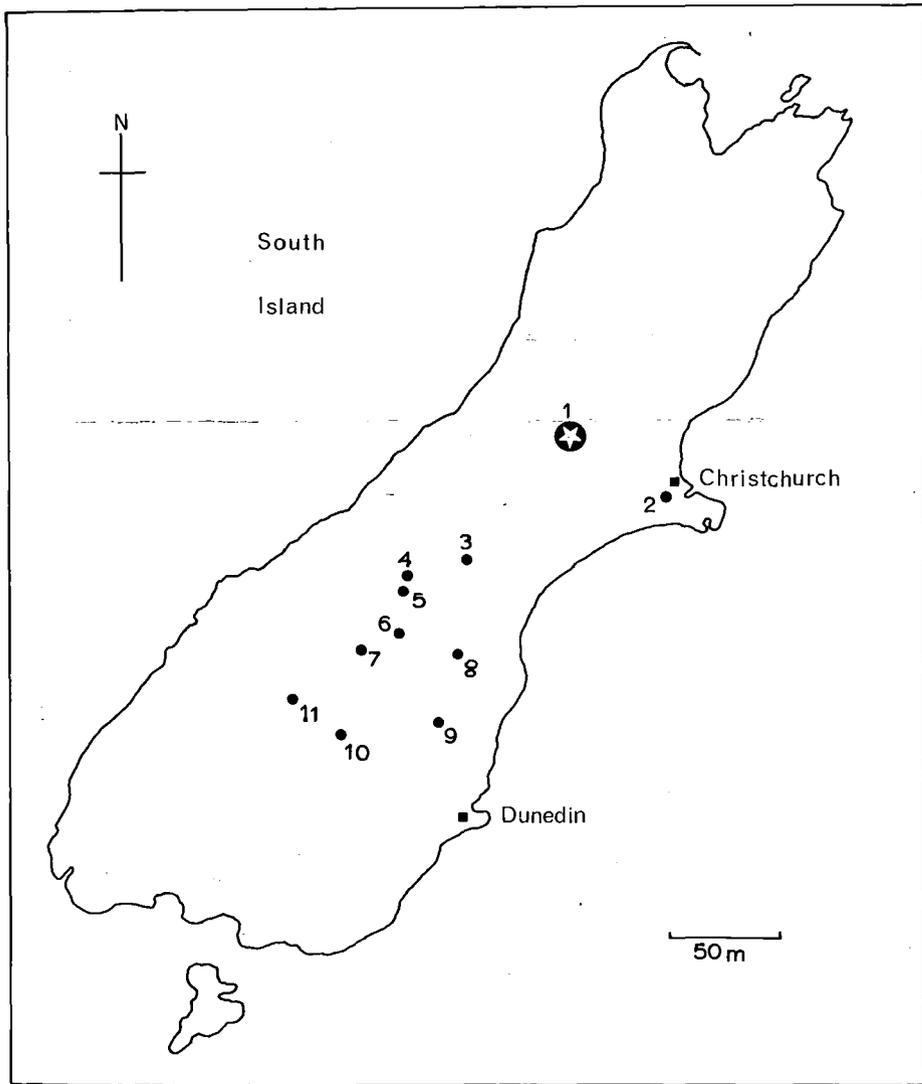
The aim of the present investigation has been twofold; to produce an outline of the autecology of sweet brier; and to provide more detailed information about certain problems, especially those concerned with establishment and survival of seedlings. Many sweet brier populations throughout New Zealand were visited and much observational data was recorded. Detailed field work was confined to the Waimakariri catchment, North Canterbury, though other South Island populations were given close attention (figure 0,1). The detailed experimental work was carried out at Lincoln College.

The seasonal activity of the species in the field was studied, and measurements were made on the growth of different plant organs in different habitats, and the reproductive capacity of populations. The survival of seed and seedlings was also followed. Some environmental factors were measured, but these were not sufficiently comprehensive to establish quantitatively the differences between any two sites, or to

Fig. 0,1.

Map of the South Island, New Zealand, showing the location of places mentioned in the text.

1. Waimakariri catchment
2. Lincoln College
3. Burkes Pass
4. Dusky
5. Rhoboro Downs
6. Omarama
7. Lindis Pass
8. Hakataramea
9. Patearoa
10. Alexandra
11. Cardrona Valley



establish a statistical correlation between plant performance and environmental factors.

Certain aspects were selected for experimentation, largely to help resolve ecological problems, and not to yield information of a basic physiological nature. The scope of experiments was limited to some extent by the difficulties involved in raising adequate stocks of seedlings at convenient times. One series of experiments tested the effects of temperature and daylength on the seasonal activity of buds, extension growth of shoots, and cambial activity. A further series studied the effects of different light climates, and different levels of soil water and aeration, exposure, and soil fertility. A large, greenhouse experiment was designed to test the effects of competition between sweet brier, grass, and clover seedlings.

The general history and taxonomic status of sweet brier are discussed in Chapter 1, and the identity of the species in New Zealand is reviewed in Chapter 2. In Chapter 3, the distribution and ecology of the species is discussed to elucidate some of the major factors which apparently limit its occurrence in this country. Then follows a description of the principal plant communities and the types of habitat within which sweet brier is found. The remainder of this dissertation attempts to develop a logical sequence, beginning with a detailed discussion in Chapter 4 of the structure, life history, and seasonal behaviour of the species as determined by its genetic constitution. Chapter 5 examines the effects of some environmental factors on seedling growth, and Chapter 6 discusses the mature plant in its natural environment. Chapter 7 is in part a synthesis; it reviews some of the more important biotic effects on seedling establishment, and attempts to

relate the conclusions drawn in preceding chapters. Some of the reasons for the extraordinary success of sweet brier in New Zealand are outlined in Chapter 8.

The literature on sweet brier is meagre, and nearly all the published work is connected with its cytology and genetics. I have not listed an extensive bibliography covering authorities dealing with accepted botanical concepts, assuming that these are well enough known not to be quoted. My use of plant names is based on Allan (1961) for indigenous vascular plants other than monocotyledons, Cheeseman (1925) for monocotyledons other than those recently revised by Zotov (1963), and Clapham et al (1962) for most introduced plants.

For cross-referencing, I have used the three-figure numbers of the subsections instead of the page numbers, and to facilitate this, the subsectional numbers are included at the top of the appropriate pages.

CHAPTER 1

HISTORY AND TAXONOMIC STATUS OF SWEET BRIER

INTRODUCTION

Sweet brier belongs to the widely dispersed genus Rosa; a well-marked group of plants which has played a large part in the medical and horticultural progress of mankind. The genus is rich and varied, and in no other have the opinions of taxonomists been so much at variance. Its probable 100-120 species are scattered chiefly throughout the temperate and subtropical zones of the Northern Hemisphere, spreading south in more recent times with the migration of European peoples. Today few countries in these zones are without their wild roses, native or introduced, but surprisingly, very few species have played more than a minor role in the development of cultivated roses. On the other hand, several species, including sweet brier, are conspicuous in the weed floras of their adopted countries.

SECTION 1. HISTORICAL RECORD111. General history

According to Willmott (1911), sweet brier was the only British wild rose permitted to rank as a garden plant, being valued for its fragrance, vigour, and hardiness. In days when all manner of conserves and pot-pourri were prepared, the hips of sweet brier were eaten as a delicacy and young shoots were candied. It was one of the 8 rose species known to classical authors, and is mentioned in the writings of Chaucer, Spenser, Milton, Shakespeare, and others. The merit of its hips as a conserve or elixir was recognised and recorded by Pliny, and ancient

herbals praised its virtues. Thus it appears to be firmly established in the historical record of European peoples.

The pre-history of sweet brier is unknown. However, some idea of its probable distribution and ecology in ancient times can be gained from a brief consideration of the fossil record of Rosa, and current views on the Late-glacial and Post-glacial history of the British flora.

Fossil roses, once considered rare, are now known to have been widely dispersed in the western United States, Asia, and Europe by Oligocene times. The earliest find dates from the Paleo-Eocene, confirming the strict limitation of Rosa to the Tertiary. These Tertiary roses had a world-wide distribution, and at various intervals intercontinental dispersal of a species was readily facilitated (Becker, 1963). Leaves and leaflets, detached thorns, and stems with attached thorns, are of common occurrence in the fossil record.

The general picture which emerges from Quaternary studies of the British flora sheds some light on the history and ecology of spiny scrub containing such species as sweet brier. Matthews (1955) includes sweet brier and the Burnet Rose, Rosa spinosissima (syn. R. pimpinellifolia), along with 80 other species of the British flora in his "Continental" element; a group of geographically related species characteristic of central Europe, thinning out westwards, but frequently extending east through Russia into Asia. Plants of this element are commonly known as "steppe" species, because the majority are calcicolous and confined to more or less open and dry habitats. However, as Pigott and Walters (1954) remark, this term has been loosely or even inaccurately applied, and is frequently misleading.

Briefly stated, the current view (cf. Pigott and Walters, 1954; Godwin, 1960) holds that continental species and many plants now behaving as weeds were widespread in Britain during the Late-glacial, when raw mineral soils and an open, tundra type vegetation prevailed. During the Post-glacial, which began about 8,000 B.C., such communities suffered widespread contraction as the Boreal birch-pine forest expanded, and became very restricted at the time of the deciduous forest maximum, surviving in habitats which precluded the development of woodland, leached soils, or peat bog. This state persisted until Neolithic forest clearance began about 3,000 B.C., after which time those species which could take advantage of an increase in area suited to them, re-extended their range. This pattern was intensified in Bronze Age, Iron Age, and subsequent time, but is complicated by considerable Post-glacial climatic fluctuations, in the course of which different species contracted or expanded their geographic range.

The occurrence of sweet brier in Britain may also date from Late-glacial time, and its present distribution and weak-stemmed habit (Tansley, 1939) is the result of micro-climatic and edaphic factors becoming less favourable. Alternatively, it may have been introduced with pre-historic agriculture and proved weakly aggressive, save on shallow soils overlying chalk. Whatever its origin, its predominantly eastern distribution and habitat preference conforms well with the concept of a "steppe" element, not only in the British flora, but in the naturalised flora of New Zealand.

112. Introduction to New Zealand

The exact origin of sweet brier in New Zealand is somewhat obscure. Hooker mentioned it in his list of plants in 1864, and it has occurred in every subsequent collector's list.

According to Thomson (1922), Darwin recorded whole hedges of sweet brier in mission gardens at Paihia, Bay of Islands, in 1835. Steen (1963) considers that it entered this country close on the heels of the historic china roses (Rosa chinensis), noting that it was raised from seed to form hedges around some of the earliest gardens in mission, milling, and mining settlements. It is certain that its anti-scorbutic properties were not known to early settlers. It flourished in the early mining settlements of Central Otago, where scurvy was rife and perhaps the miner's greatest enemy. Thomson (1922) believes that it was introduced purely for sentimental reasons. "The early settlers everywhere planted this favourite shrub, as a hedge plant, and everywhere, at least in the North Island, it got away from cultivation and quickly established itself, as a plant most difficult to eradicate."

Guthrie-Smith (1953) includes sweet brier in his list of plants naturalised between 1892-1902 on "Tutira" station in the province of Hawkes Bay. "Missionary", as it was then called, "has been spread abroad by the horse and as its local name implies is a child of the Church of England, along with such familiar plants as peach, cherry, spearmint, thyme, horehound, thornapple, willow, and even ryegrass."

The popularity of sweet brier as one of the first hedge plants on pastoral land in the South Island was mentioned by Anderson (1916).

Ample supplies of plants were obtained from Tasmania for this purpose, and it was advertised for sale, along with gorse, thorns, and privets by a Christchurch nurseryman in 1855. Although live plants were imported to this country, the chief method of entry was probably by seed. This supposition is in line with the widespread occurrence of the rose seed chalcid, Megastigmus aculeatus, in sweet brier populations throughout New Zealand. The life history of this wasp-like parasite is entirely dependent upon flowering and seed setting in its preferred host sweet brier, in whose seed it could only have entered this country.

Thus the introduction of sweet brier to New Zealand was not accidental or fortuitous and, as with most of our prominent weeds, its entry is closely associated with the migration of peoples from the Northern Hemisphere. There is little doubt that it reached many parts of New Zealand in rapid time, either directly from nurserymen or mission stations, or by more circuitous routes from the same sources. Its subsequent spread has been effected mainly by grazing animals, both wild and domestic, and by the introduction and multiplication of fruit-eating birds such as the thrush and the blackbird. Its weedy tendencies were realised in the earliest days of settlement, and in 1900 it was classified with blackberry and Californian thistle in the first schedule of the Noxious Weeds Act. In this country its hips now provide the principal source of vitamin C, the anti-scorbutic vitamin.

SECTION 2. (121) SURVEY OF TAXONOMIC TREATMENT

Botanically sweet brier is recognised as a widespread pentaploid rose whose closest ally in this country is the Dog Rose, Rosa canina. The latin name for sweet brier has been less stable than the common names (eglantine, sweet brier), and both of Linnaeus' epithets, eglanteria and rubiginosa, have been used by various authorities.

It appears that Linnaeus (Species Plantarum, Vol. i, p. 491, 1753) confused sweet brier with a yellow-flowered rose, R. foetida. The specimen in the Linnean herbarium labelled Eglanteria is undoubtedly R. foetida (Willmott, 1911), an error which Linnaeus apparently realised, for in 1771 (Mantissa ed. 2, p. 504) he called sweet brier, R. rubiginosa, reserving the epithet Eglanteria for his yellow-flowered specimen. Thus, according to the Code of Nomenclature, the name R. rubiginosa should stand as the earliest valid name for the species.

Woods in 1818 (ex Willmott, 1911) and Willmott rejected Linnaeus' change of epithet, claiming priority for eglanteria, but most 19th century systematists agreed with Linnaeus. At present a number of authorities, mostly American (e.g., Rehder, 1940) prefer eglanteria, probably following Willmott's (1911) vindication of Woods. However, most British and European authorities use rubiginosa.

I have followed the treatment of Dandy (1958), who prefers rubiginosa and places eglanteria in the category of misapplied epithets.

The arrangement of sweet brier in a formal classification of Rosa involves less argument. There have been many attempts to classify the genus with more or less satisfactory results. The arrangement proposed

by Crepin is considered the most natural and is generally accepted by European authorities. Wylie (1954a), however, considers that Rehder's (1940) classification agrees reasonably well with the available cytogenetical facts, and uses it in tracing the history of garden roses. In the following arrangement I have adopted the treatment of Clapham et al (1962), which is essentially a slight modification of Crepin's scheme.

Family:	ROSACEAE Juss.	Rose family
Subfamily:	ROSOIDEAE	
Tribe:	ROSEAE	
Genus:	ROSA L.	Rose
Subgenus:	EUROSA Focke	Roses proper
Section:	CANINAE DC.	Dog roses
Subsection:	RUBIGINOSAE Crepin	
Species:	Rosa rubiginosa L.	Sweet brier

CHAPTER 2

NEW ZEALAND FORMS AND HYBRIDS

INTRODUCTION

A first requirement in an autecological study of any species is a practical taxonomic arrangement so that various specimens can be given names and referred to categories which can be interpreted without ambiguity. It should be based preferably on characters identifiable in the field. The occurrence of forms or varieties of an aggregate or widespread species must however be considered, as the segregates may have ecological preferences which can easily be overlooked in a consideration of the aggregate.

Most investigators up to the present agree that the genus Rosa is a freely interbreeding and polymorphic group. Further, the environmental influence on taxonomic characters is considered so strong that it is difficult to separate the various forms into satisfactory groups. In the section Caninae polymorphism is supposedly rife, resulting in a large number of so-called "microspecies". According to Gustafsson (1944), it reaches an extreme in the subsection Eucaninae (including the Dog Rose, Rosa canina), but R. rubiginosa varies very little in nature and produces uniform progenies, at least in Scandinavia.

In this chapter the identity of the introduced forms and putative hybrids of sweet brier is considered.

211. Field observations

Many populations of sweet brier throughout New Zealand were visited in the course of general observations. These and numerous isolated

individuals were examined from the following viewpoints:

- (1) To decide on the number of rose species present.
- (2) To record any variation within and between populations and individuals.
- (3) To collect live material for laboratory analysis.
- (4) To collect open-pollinated seed from as many different habitats and geographic areas as possible for progeny testing.

To supplement this widespread survey, a more intensive sampling procedure was adopted, and experiments were carried out, in 4 populations in the Waimakariri catchment, namely at Dry Creek, Flock Hill, Lake Pearson, and Cora Lynn. In addition to my own observations, much live material was received from Farm Advisory Officers of the Department of Agriculture, stationed throughout the country. Finally, specimens in several of the large herbaria were examined, and cultivated plants in the rose species section of the Christchurch Botanic Garden were studied.

It was intended to examine all this material from as many points of view as possible, and in the event of genetic variation, to establish broad categories which would give some meaning to the species in New Zealand. As a result of these investigations the following conclusions are drawn.

Several species of Rosa are reputed to exist in this country, but the two canine species, Dog Rose (R. canina) and sweet brier (R. rubiginosa) are the only wild roses of any significance. There are no particular problems in distinguishing these two as they occur in New Zealand. The Dog Rose is quite distinct morphologically from sweet brier (figures 2,3 - 2,6; table 2,1). Furthermore, the two species are ecologically

differentiated. The Dog Rose is sparsely distributed throughout the country and could hardly be described as a weed. It seems to be confined to areas of high rainfall (> 35") in grassland environments. Sweet brier, however, has a much wider ecological and geographical amplitude, so that their distributions overlap in places. Since the two species are known to hybridise when given the chance, at least in cultures, spontaneous hybrids should occur. However, such hybrids are comparatively rare in this country. The only populations that I know in which it looks in the field as if hybridisation occurs are in the Cardrona Valley, Central Otago, and at Cora Lynn - Bealey in the Waimakariri catchment (215).

Over large stretches of country sweet brier appears as one normal form with no significant genetic variation. This form is certainly the most widespread and abundant, and its morphology conforms well with the description of Rosa rubiginosa in the British Flora (Clapham, et al 1962). I have tentatively called it "N type" brier (figure 2,1). As is to be expected with a species which is able to survive in diverse habitats and through such a wide geographic range, there is a considerable amount of variability, mainly in the size, colour, and texture of individual organs, and phenology. That this is due to local differences in environment and is not genetically fixed can be demonstrated in transplant experiments. An example quoted by Erlanson (1930), which I am able to confirm, is the simultaneous flowering of cultivars from diverse geographic regions.

Another, hitherto unknown, abnormal form coexists with N type brier in certain localities and it usually exceeds the latter in overall

dimensions. It is more restricted geographically and occurs at much lower frequencies in local populations. The approximate number of mature plants at Dry Creek, Flock Hill, Lake Pearson, and Cora Lynn is 5, 20, 25, and 38 respectively, out of a total of many hundreds of N type individuals. The fact that the rainfall increases from Dry Creek (36") to Cora Lynn (60"), suggests a preference for wetter conditions. From the taxonomic viewpoint it can still be referred to Rosa rubiginosa, though it has some "non-rubiginosa" features. I have tentatively called it "A type" brier (figure 2,2).

No morphological intermediates were observed in the field, either between the putative hybrids and their supposed parents, or the principal forms of sweet brier, but at Dry Creek two additional aberrants are known. The distinguishing features and relationship of these forms and hybrids are discussed in the following subsections.

212. Morphology

As mentioned above (211), only two forms of sweet brier have objective reality in this country. Although they both correspond to the classical description of Rosa rubiginosa, the aberrant form is far less typical. Nor does it seem to fit any of the English varieties described by Wolley-Dod (1930). A description of each form is given below.

N type sweet brier (figures 2,1, and 2,3-2,6):

Deciduous shrub reaching an extreme height of 5 m, but usually 1-3 m. Stems erect at first, later arching, armed with stout, hooked,

Fig. 2,1.

Habit of a typical N type brier plant at Flock Hill.

Fig. 2,2.

Habit of an A type brier plant in the Cardrona Valley.



Fig. 2,3.

Flowers: Left to right - Dog rose, N type brier,
A type brier (c. $\frac{1}{2}$ natural size).

Fig. 2,4.

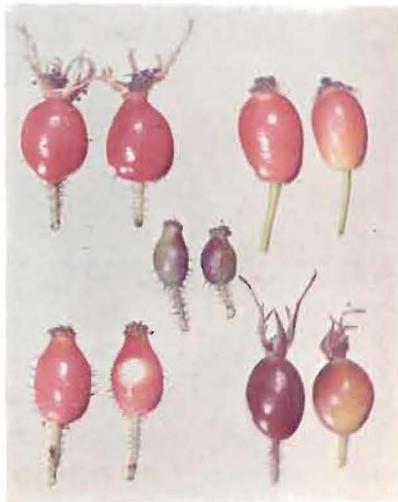
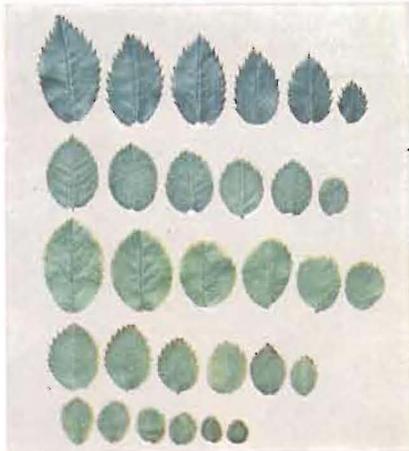
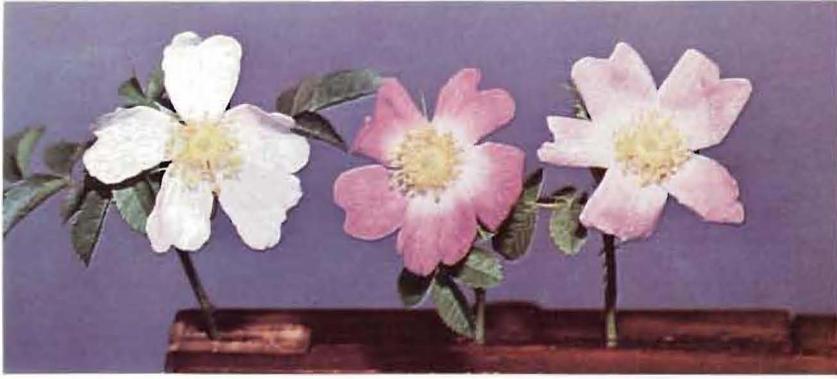
Canes: Left to right - Dog rose, N type brier,
A type brier, fertile hybrid (rubiginosa
x canina), sterile hybrid (canina x rubiginosa)
(c. $\frac{1}{3}$ natural size).

Fig. 2,5.

End leaflets: Top to bottom - Dog rose,
N type brier, A type brier,
fertile hybrid, sterile hybrid.
(c. $\frac{1}{2}$ natural size).

Fig. 2,6.

Hips: Top left to bottom right - N type brier,
Dog rose, sterile hybrid, A type brier,
fertile hybrid ($\frac{3}{4}$ natural size).



unequal prickles mixed with scattered aciculi and setae. Leaflets 2-3 (-4) pairs, 1-2 (-4) cm, suborbicular to oval-elliptic, \pm rounded at the base, doubly glandular-serrate, pubescent on veins above and beneath, very glandular beneath. Flowers 1-3 (-5) or more, bright pink, with regular opening. Pedicels 1-1.5 (-2) cm, glandular-hispid. Sepals 1-2 cm, erect or spreading after flowering, persistent until fruit ripens. Petals 1.5-2 cm or more. Styles free, short, pilose. Fruit subglobose to ovoid, 1.5-3 cm, scarlet, usually smooth but sometimes glandular-hispid at the base, rarely bristly all over.

A type sweet brier (figures 2,2-2,6):

Tardily deciduous shrub reaching an extreme height of 7 or 8 m, but usually 3-5 m. Stems \pm arching, richly branched and cymose due to precocious development of axillary buds, armed with stout, hooked, usually equal prickles. Leaflets 2-3 (4) pairs, 1-2 cm, suborbicular, rarely oval-elliptic, rounded at the base, glandular-serrate-crenate, sparsely pubescent on veins above and beneath, glandular beneath. Flowers 1-3, pale pink, with irregular opening. Pedicels 1-1.5 cm, glandular-hispid. Sepals 1-2 cm, reflexed after flowering, readily deciduous. Petals 1-1.5 cm. Styles free, short, thinly pilose. Fruit urn-shaped, 1-2 cm, scarlet, bristly all over.

Morphological characters of both forms were scored during the active and dormant seasons using the score sheets adopted by the British Rose Survey in which 36 of the most useful taxonomic characters are listed with contrasting descriptions. The dimensions of leaves and flowers were derived from large samples selected at random from the 4 Waimakariri populations. An air-flow planimeter constructed after that described by

Jenkins (1959) was used to measure leaf and petal areas.

Certain features of both forms show considerable variation, so much as to overlap, e.g., dimension of organs. Others seem to be constant enough to be valuable in delimiting the two. The chief taxonomic characters that distinguish these forms and the Dog Rose in this country are set out in Table 2,1.

The two unnamed aberrants at Dry Creek differ from both main forms as well as from each other. One is a vigorous plant resembling N type plants which surround it, but its flowers are much smaller and brilliant pink in colour, its hips are globose and smooth, and its pedicels are totally eglandular; a feature hitherto not seen in sweet brier. In all other respects it tallies with N type brier. The other form is situated next to a mature A type plant, and is notably lacking in vigour, with a high proportion of dead canes and branches. It has the same marked heterocanthly of N type plants, and bears very few, pale pink flowers. Its hips are irregularly globose and smooth, but its sepals drop much earlier than any form seen. It scored a preponderance of A type characters.

213. Cytology

Both sweet brier and the Dog Rose are pentaploids. Tackholm (1922) gave the somatic chromosome number of both species as 35. The basic number for the genus is 7, and all polyploid levels up to enneaploid ($2n = 63$) have been described. Triploids, heptaploids, and enneaploids are known only in a few hybrids and never among wild species (Rowley, 1960).

The canine rose species differ from all other roses by their unique behaviour at meiosis, a fact first pointed out by Tackholm (1922), and subsequently confirmed by other rose cytologists (cf. Wulff, 1955). They are all polyploids with 28, 35, or 42 somatic chromosomes, and show only a minimum amount of chromosome conjugation at meiosis. In all cases they form only 7 bivalents and 14, 21, or 28 univalents.

The behaviour of these univalents in meiosis leading to microsporogenesis is entirely different from that in megasporogenesis. In the former, the univalents are either entirely lost or form non-functional pollen grains, whereas the 7 bivalents undergo normal reduction division and form functional pollen grains with 7 chromosomes. Thus there is a high proportion of sterile pollen.

In megasporogenesis, on the other hand, all the univalents and 7 chromosomes from the bivalents are included in the two upper megaspores in the ovary. The uppermost one alone is functional, and the resulting embryo sac and egg cell has $2n - 7$ chromosomes. Thus in sweet brier and the Dog Rose which possess 35 somatic chromosomes, the pollen grains have 7 and the egg cells 28. Self-fertilisation must then result in progeny in which the normal somatic number of 35 is restored. From the genetic viewpoint, this peculiar meiotic behaviour - the so-called "balanced heterogamy" - combined with self-pollination, means that all pure species of canine roses breed true. Likewise, since the pollen grains of all canine roses contain 7 chromosomes, the somatic number of all hybrids, canine rose x canine rose, must always equal that of the seed parent. Their behaviour is therefore strongly matroclinous, and progeny resemble the seed parent rather than the male (215).

There have been several theories explaining this unique meiosis in canine roses. These have been discussed and subsequently rejected by Blackhurst (1948), who suggests that the most likely explanation is that of control through an allelomorphic series of meiosis-regulating genes; a view which so far has not been challenged.

My attempts to study meiosis in both N type and A type brier proved unsuccessful, as also were somatic counts of seedling root tips, despite the fact that satisfactory techniques are known (e.g. Wylie, 1954b). The chromosomes are very small and proved difficult to stain. Also they tended to stick together, which made counting extremely hazardous and unreliable. This failure to produce satisfactory preparations prevented a proper interpretation of the status of the two main forms.

In the absence of cytological confirmation, two alternate hypotheses are advanced to account for the origin of the main aberrant form - A type brier.

- (1) Either it is a chance hybrid between the Dog Rose and sweet brier, or
- (2) It is an aneuploid, with a chromosome number deviating from the normal 35 by 1 or more.

The origin of A type brier through hybridisation is the least likely even bearing in mind the long-lived character of canine roses, and the possibility of the hybrid surviving long after one parent had vanished. A type brier coexists with N type brier in areas far removed from the nearest Dog Rose, and in habitats inimical to the survival of the latter. The supposition that one parent has vanished (in almost every case this would have to be the Dog Rose) can be dismissed, likewise

the chance of long range (and random) dispersal of selfed A type seed. Finally, A type does not tally with known hybrids.

The second hypothesis is the more probable one. Aneuploids are not unknown in Rosa, though they are apparently rare. The canine roses provide more than half the known examples, especially in the pentaploid group, the best source being experimental progenies of wild species (Rowley, 1960). Shahare and Shastry (1965) found that 5 out of 96 varieties of non-canine garden roses were also aneuploids.

So far no aneuploids have been recorded in the wild, but this is fortuitous, probably due to inadequate sampling. In the John Innes collection of rose species, there are two fully fertile plants of sweet brier with both 35 and 42 chromosomes, but no proven aneuploids (Rowley, pers. comm.). In his studies of aneuploidy Rowley (1960) comments thus:

- (1) Chromosome variation in progenies is always associated with phenotypic variation.
- (2) Aneuploids show no tendency to revert to euploids in the germ line, and in one case tested breed true for their somatic number.
- (3) Aneuploids are not necessarily weaker in straight competition with euploids.
- (4) There was a clear indication of reduced fertility with chromosome loss.

These comments are in line with the character and behaviour of A type brier (214).

The origin of the other two aberrants at Dry Creek can only be speculated on at this stage. They may be progeny of either A type or N type, or chance hybrids between the two (215).

214. Breeding system

Early cytologists (e.g., Tackholm, 1922) concluded that the canine roses were reproducing by apomixis because of their abnormal meiosis and high degree of pollen sterility, together with the fact that pure species tended to produce progenies which were morphologically and cytologically uniform and resembling the maternal parents (Wulff, 1955).

Tackholm and others have shown that meiosis leads to pollen grains with 7 chromosomes and egg cells with the somatic number minus 7. Therefore, canine rose seedlings with the full somatic number cannot arise by parthenogenesis from an unfertilised egg cell. This led the early cytologists to conclude that whatever cell produced the new seedling, it must be somatic in origin. However, subsequent embryological studies failed to prove that this type of apomixis occurred. Likewise, experimental removal of anthers did not yield positive results in support of apomixis. The few instances reported of seed set following emasculation are generally attributed to faulty technique, and not to parthenogenesis or the production of accessory stamens. Finally, hybridisation experiments clearly indicate that canine roses do possess functional pollen grains and embryo sacs (215). It appears, therefore, that pollination is necessary in canine roses and their hybrids.

In this study certain aspects of the breeding system of the two main forms of sweet brier were investigated and several interesting features were noticed.

Self-pollination mechanism:

In both forms of sweet brier the petals unfold when they are very small, and increase in size during the flowering period. This character Macfarlane (1963) calls "precocious petals". Many flower buds of A type brier showed poor or irregular opening, and an even greater number failed to open at all; a feature not observed in N type brier. In both forms the petals are usually past their prime on the third day and some have already begun to fall (411). The stamens then rise and curve over the receptive stigmatic dome, and most of the pollen is shed. This mechanism of self-pollination was consistently observed in both forms with regular flower opening, and has been noted to take place in the absence of insects. It is suggested, therefore, that sweet brier is strongly selfing and not weakly selfing as Macfarlane (1963) records.

Pollen studies:

The second interesting feature is the marked contrast in pollen fertility between the two main forms. The method of collecting and preparing pollen is outlined in Appendix 2,1; the amount of functional pollen being determined by the differential staining technique described by Owczorzak (1952).

Functional grains of N type pollen are fairly uniform in size and shape. They are mostly 3-colpate, but 4-colpate grains (the largest) are not uncommon (figure 2,7). The average amount of functional pollen

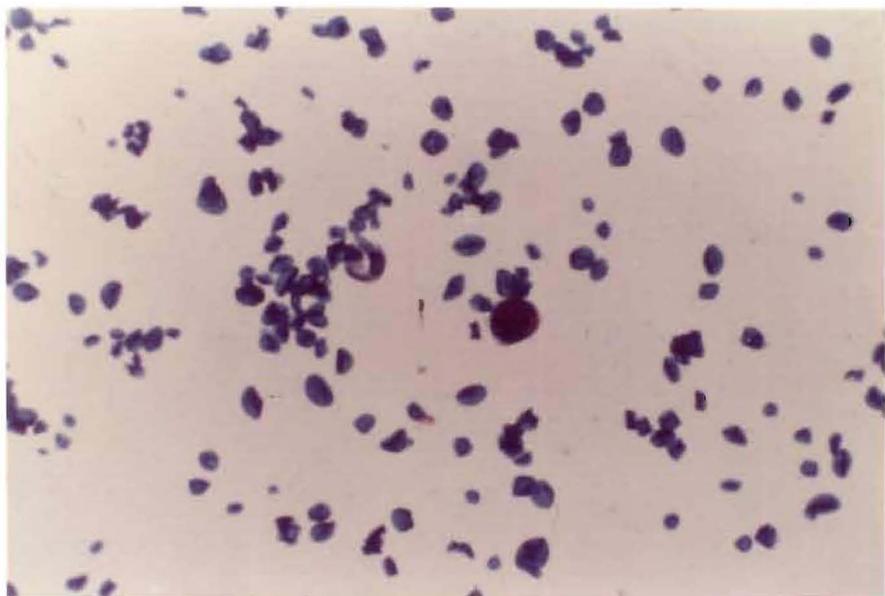
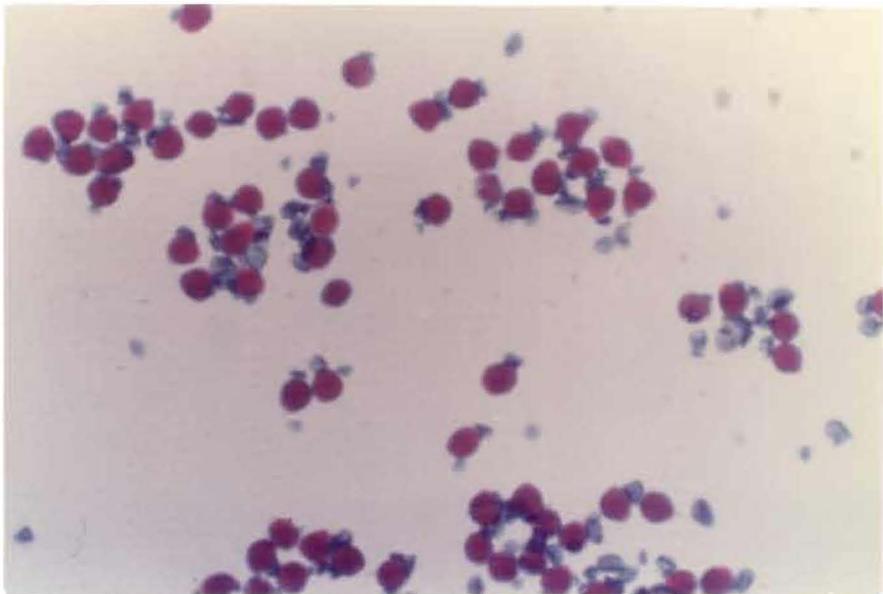


Fig. 2,7.

Pollen of N type brier. Functional grains stained red, non-functional blue-green (x400).

Fig. 2,8.

Pollen of A type brier. Functional grains stained red, non-functional blue-green (x400).

in the 4 Waimakariri populations in 1962-63 was 28.2%, with an extreme range over the two years of 25.0 - 33.0%; figures which compare more than favourably with counts for Rosa rubiginosa obtained by Flory (1950), e.g., average 28.2%, range (over 2 years) 22.5 - 38.8%.

The pollen of A type briar, on the other hand, is highly sterile, and as a rule only 1 or 2 functional grains per flower were observed among several thousand aborted grains (figure 2,8). In some flowers though, up to 10 or 12 functional grains were observed.

These outstanding contrasts in pollen fertility account for the differential seed set recorded in the two main forms (figures 2,9 and 2,10, and table 4,5), and reinforce the view that self-fertilisation is the principal method of sexual reproduction. Very few N type flowers fail to produce seed under average field conditions, but a large number of A type hips wither and drop because of the preponderance of sterile pollen and the failure of the egg cells to become fertilised.

At this point it should be noted that the other two aberrant forms at Dry Creek follow a similar pattern; the one resembling N type briar is equally fertile, the one resembling A type briar is just as sterile.

Breeding experiments:

The following procedure was adopted in emasculation and hybridisation experiments in 1962 and 1963. In the former, the corolla and stamens of the unopened flower bud were removed with tweezers, and the treated bud was isolated in a synthetic sausage casing supported on the inside by a spiral piece of insulated wire, and sealed at both ends by a pad of cotton wool and wire, paper clips. Untreated (selfed) buds were bagged in the same way, and open-pollinated flowers were merely tagged.

Fig. 2,9.

Sectioned hips: Top left to bottom right - N type brier,
Dog rose, sterile hybrid, A type brier,
fertile hybrid (about natural size).

(Courtesy N.Z.J. Agric. 109: 1964)

Fig. 2,10.

Achenes dissected from above: Top left to bottom right -
Dog rose, N type brier, sterile hybrid, fertile hybrid,
A type brier (x2 approx.).



Before crossings were attempted, unopened flower buds of selected pollen parents were collected beforehand and allowed to dry in paper envelopes. Crossing was obtained by removing the dry corolla and dusting the pollen on emasculated maternal parents, and bagging as in above.

On 18 December the following preliminary tests were carried out at Flock Hill. In both forms of sweet brier 20 emasculated buds, 20 selfed buds, and 20 open-pollinated buds were tagged and observed. Also 10 crossings were effected; 5 N type x A type, and 5 the reciprocal cross. One week later, most of the selfed and open-pollinated hips were visibly swelling except the selfed A type hips. Emasculated buds of both forms had begun to wither, as also were the crossings N type x A type. At subsequent intervals all the selfed A type hips withered and dropped, together with a few selfed N type hips. On 13 March all intact, tagged hips were collected and their contents examined.

Of the original N type flower buds, all the open-pollinated flowers had set seed, averaging 17/hip; 17 selfed flowers set seed, averaging 12/hip; and all the emasculated flower buds had aborted. Of the original A type flower buds, 12 open-pollinated flowers set seed, averaging 4/hip, and all the selfed and emasculated flower buds had aborted. N type x A type crossings failed to set seed and aborted, but 3 hips of the reciprocal cross set seed, yielding 16, 22, and 20/hip.

These tests were repeated in 1963 at the same site, and in addition, the Dog Rose was used as the male parent in crossings with both forms of sweet brier. Much the same results were achieved, but 4 selfed A type hips set seed, yielding 3, 2, 3, and 1/hip. The cross A type x N type was again successful, 4 hips yielding 15, 19, 21 and 17 seeds/hip, and

the reciprocal cross was unsuccessful. All crosses A type x Dog Rose and N type x Dog Rose were successful, the hips averaging 15 and 17 seeds respectively.

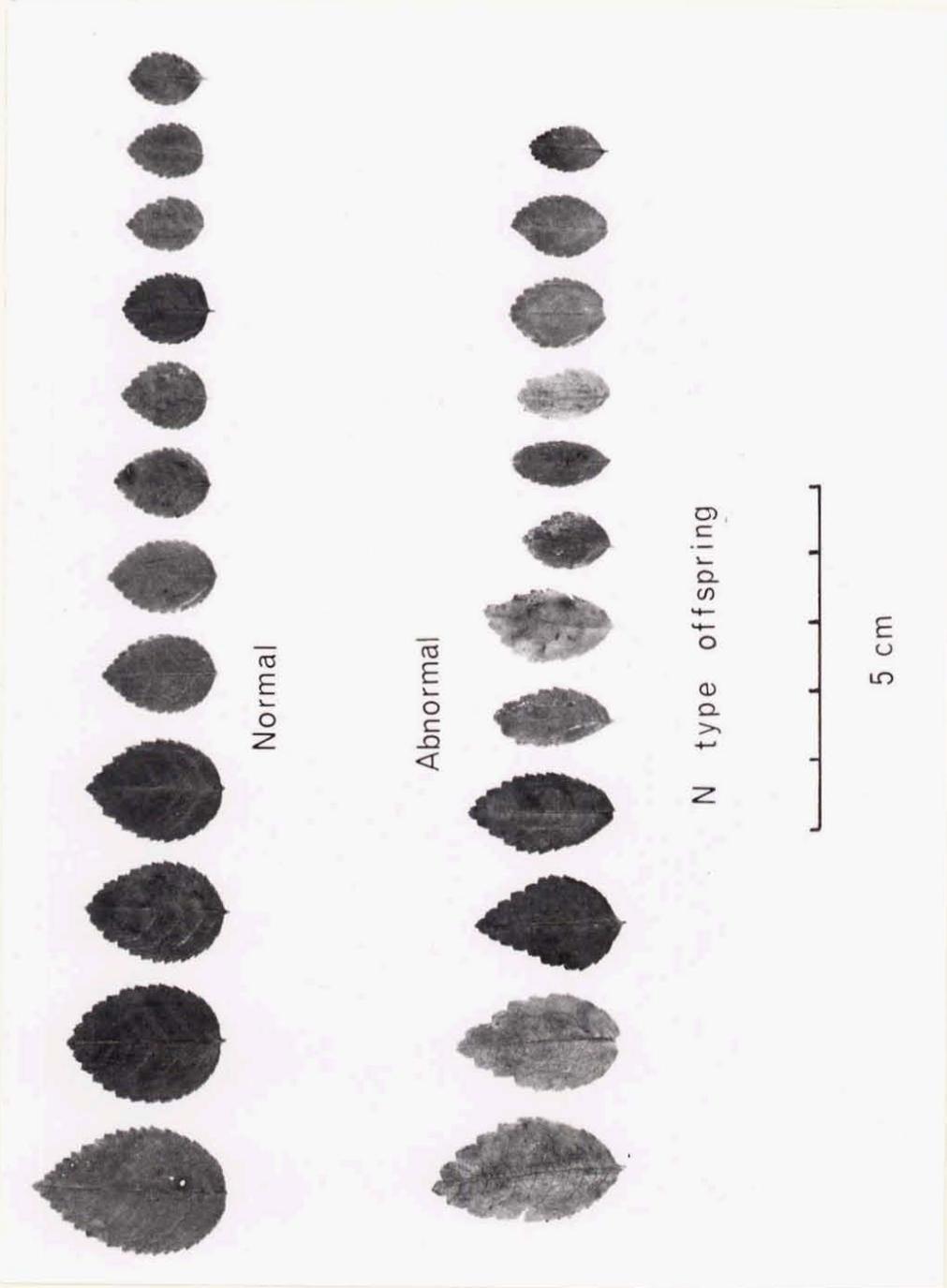
These results may be summarised as follows:

- (1) The sex cells of both forms are functional.
- (2) In both forms pollination is necessary.
- (3) Both are self-fertile in spite of severe reductions in fertilisation with artificial selfing, and self-fertilisation is very common.
- (4) The artificial cross A type x N type is successful but the reciprocal is not.
- (5) Both forms will accept artificially applied Dog Rose pollen.

Sowings of wild, N type seed as a rule produce uniform progenies which rarely transgress the limits of the form or species (figure 2,11). From what has been discussed, this is brought about by the peculiar meiotic behaviour, or balanced heterogamy of the species, combined with a high incidence of self-pollination. Even if insect pollination occurred (as it most certainly does in many areas), the homogeneity of the breeding unit remains unaffected. Occasionally, however, some abnormal or aberrant plants arise from cultured N type seed (figure 2,11).+ Nearly all of these are "runts" and most probably would be eliminated in straight competition in the wild (cf. Rowley, 1960), i.e., all except A type brier which is assumed to be the most successful derivative. The inference here is that all aberrant N type progeny are likely to be aneuploids.

Fig. 2,11.

End leaflets of normal and abnormal progeny of
N type brier.



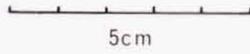
29a

Fig. 2,12.

End leaflets of N type and A type brier progenies.



N type offspring



A type offspring



Progeny of wild A type seed are extremely heterogeneous (figure 4,12). Some resemble N type plants in seedling morphology, but most are "runts" with limited survival value. Such progenies are at present being cultivated for intensive study.

215. Natural hybrids

The spontaneous occurrence of canine rose hybrids is now an established fact. Early systematists rarely mentioned them, but from both morphological and cytological evidences we are obliged to admit their existence. Failure of the early taxonomists to recognise this fact led to much confusion in the classification of canine roses and their hybrids.

Most of the information concerning hybridisation has arisen from experimental studies. At present three types of artificially produced hybrids are known:

- (1) Hybrids between canine species (Gustafsson, 1944; Blackhurst, 1948).
- (2) Hybrids between canine species as female parents and "normal" roses as male parents (Blackhurst, 1948).
- (3) Hybrids from crosses reciprocal to (2) (Fagerlind ex Wulff, 1955).

Wulff (1955) describes the prominent features of each type of hybrid from the viewpoint of the breeding system in the section Caninae. He sums up by stating that all the research hitherto done on them confirms

that balanced heterogamy and self-pollination provide a satisfactory explanation for the true-breeding character of the pure canine rose species.

It is proposed to discuss only the first type of hybrid (canine rose x canine rose) for two reasons. First, because it is believed that it is the only type to occur in this country, and second, it has been demonstrated already (214) that both forms of sweet brier will accept Dog Rose pollen.

As mentioned previously (213), the canine roses are unique among roses, indeed most plants, in the unequal contribution which the two parents make towards their progeny. For example, if the Dog Rose is pollinated by sweet brier, the offspring are very similar to though not identical with the mother. The same condition emerges in offspring of the reciprocal cross. But contrary to the cytological behaviour of the pure species, these hybrids usually show a decreased number of bivalents resulting in a disturbed meiosis and fertility. Thus the true identity of these hybrids should be evident from their morphology, and more particularly from the behaviour of the chromosomes at meiosis.

In this study I attempted to establish the identity of putative hybrids between sweet brier and the Dog Rose solely on morphological grounds. Both Gustafsson (1944) and Blackhurst (1948) produced offspring from sweet brier x Dog Rose, and the former has also raised offspring from the reciprocal cross. Blackhurst was concerned primarily with cytogenetic aspects rather than with morphological features. Gustafsson's account is far more informative in the latter respect and was used extensively to match putative hybrids in the Waimakariri catchment.

Gustafsson's observations can be summarised as follows: When the Dog Rose is the maternal parent the F_1 plants show the following features:

- (1) Pronounced heterogeneity (aneuploids occur).
- (2) Resemble the mother in most vegetative characteristics.
- (3) Leaves, stipules, and sepals are glandular, but not with the rich glandulosity of sweet brier.
- (4) Persistent sepals.
- (5) Petal colours range from white to pink.
- (6) High sterility - 3 seeds/hip (due to irregular meiosis).

When sweet brier is the mother-plant the F_1 plants differ in almost all respects from progeny of the reciprocal cross and, according to Gustafsson, show these features:

- (1) Striking homogeneity.
- (2) Resemble the mother in most vegetative characteristics.
- (3) Stems less heterocanthus than the mother.
- (4) Deciduous sepals.
- (5) Petals whitish or pale pink.
- (6) High fertility - 15 seeds/hip (normal meiosis).
- (7) Precocious development of axillary buds giving the plants a ramosse appearance.

The latter cross consisted of 58 individuals and only one was aberrant; it was highly sterile ($2n = 34$). Apart from this plant, most of the progeny reproduced each other completely.

In my study, the two most important diagnostic features in the field were the conspicuous matrocliny, and the general infertility in the Dog

Rose x sweet brier offspring, contrasting with the general fertility in the reciprocal direction.

Between Cora Lynn and Bealey in the Waimakariri catchment both sweet brier and the Dog Rose occur together, though the latter is less numerous. There is a small number of individuals, perhaps no more than 30, which clearly match Gustafsson's Dog rose x sweet brier hybrids in most respects, except that the sepals are deciduous like the Dog Rose. There is an even greater number resembling Gustafsson's reciprocal cross in almost every detail, except that the petals are bright pink and the sepals are persistent, thus resembling sweet brier. There seems little doubt that these plants represent successful crossings. This is suggested by several vegetative characters (figures 2,4 - 2,6; 2,9 - 2,10). However, final confirmation must await more detailed field, experimental, and cytogenetic studies. One fact clearly emerges. There is not at present any indication of the polymorphism and complications that occur in hybrid populations in Britain and Scandinavia, but given time and the opportunity it could arise.

The position in the Cardrona Valley is not as clearly defined. There are numerous individuals there which match Gustafsson's sweet brier x Dog Rose hybrids, particularly in vegetative characters, ramose appearance, and high fertility, but they behave differently from their counterparts in the Waimakariri catchment. I assume that a different form of the Dog Rose is the pollen parent, but attempts to locate the parent have proved unsuccessful. It may well be a case where the progeny of a sweet brier - Dog Rose cross has reproduced itself successfully and persisted long after the pollen parent has vanished.

216. Discussion

Wild populations of canine roses in this country provide a natural laboratory for elucidating many problems of the genetics of the section which have caused so much controversy in the past. So far only two rose species of importance have been detected in the wild, namely the two canine species, sweet brier and the Dog Rose. Both can be distinguished on morphological and ecological grounds.

The oft-quoted constancy of European representatives of sweet brier is confirmed by representatives in this country. However, this constancy is not complete, suggesting that the balanced heterogamy act seldom runs undisturbed, and at least two forms constantly appear in the wild. One is a normal, fertile form which conforms with published descriptions of the species, and the other is a male-sterile, aberrant form. For the purpose of field and experimental studies, I have given them tentative names, and outlined their chief distinguishing features. Until meiosis in the two forms can be analysed, it is not possible to decide finally whether the aberrant form has arisen through hybridisation, or whether it is an aneuploid without necessarily involving hybridisation. The evidence seems to favour the latter view. Whatever its origin, the aberrant form has emerged as a successful though minor form which is superior to the normal form in vigour and vegetative growth, but inferior in reproductive capacity.

At present, nothing new can be added to published information concerning canine roses. My observations and experiments confirm that both the main forms of sweet brier are sexual and self-fertile, but not exclusively self-pollinated. There is good evidence that inter-

subsectional hybridisation between sweet brier (subs. Rubiginosae) and the Dog Rose (subs. Eucaninae) is easily accomplished artificially, and is actually taking place in the field. Cross combination leads to plants with reciprocal differences in morphology, phenology, and degree of sterility. The true hybrid nature of these plants is evident from the published descriptions of artificial hybrids. Thus it is distinctly possible that populations of multifarious forms could eventually arise both from segregation and hybridisation of existing forms of sweet brier, as well as from intense inter-subsectional crossing with the Dog Rose.

There are no apparent differences in ecology, except where the two species are concerned. All the forms and hybrids so far detected do not show any ecological preferences. From the agricultural viewpoint, they all appear to be equally susceptible to conventional measures of control and eradication. Of greater ecological significance is their extraordinary success in the introduced flora. Stebbins (1951) offers a plausible explanation to account for this fact. He agrees with most investigators in assuming a hybrid origin for sweet brier (and other canine roses) and considers it to be a heterogamous, polyploid, permanent hybrid which owes its success and aggressiveness to the permanent possession either of hybrid vigour or a favourable combination of genes. In what subsequently follows, it should be apparent that both factors are concerned.

CHAPTER 3

SWEET BRIER AS A COMPONENT OF THE VEGETATION

INTRODUCTION

One of the aims of an autecological study is to determine the distribution of a plant and the kinds of plant communities it enters and maintains itself in. This chapter describes the distribution of sweet brier with particular reference to the South Island, New Zealand. Some of the principal plant communities with which it is associated are briefly discussed to establish the relationship of sweet brier to the indigenous flora and the conditions of the various habitats. The successful interpretation of autecological studies is largely dependent on this knowledge of field ecology, not only of sweet brier, but of its associated plants and animals.

SECTION 1. GEOGRAPHICAL AND ECOLOGICAL DISTRIBUTION311. World distribution

Two aspects are concerned in the world distribution of sweet brier. One is its so-called natural distribution, the other is its extent of dispersal by human agencies beyond the limits of its natural occurrence.

It is often difficult to determine the natural distribution of plants which have been closely associated with the migration of peoples. Sweet brier is no exception. It is considered to be a native of Europe and possibly parts of western Asia. It is widespread in central Europe, gradually thinning out at all points except in the southeast. It extends north into southern Scandinavia and Esthonia, west into the British Isles, south into Spain and Italy, and east into Macedonia and the Caucasus.

From here it extends through western Asia into Afghanistan and the drier parts of the inner Himalaya, and into western Tibet (Hooker, 1879).

According to Perring and Walters (1962), it is widespread in the British Isles, but is absent from several vice-counties, especially in northern Scotland and western and central Ireland. It is more common and locally abundant in the south and east of England. Clapham et al (1962) consider it an introduction in many of its localities in the British Isles.

Throughout its natural occurrence it generally occupies land of low elevation, and is essentially a plant of open habitats. In England it is an important component of chalk scrub and is considered to be calcicolous, (Salisbury, 1952). Of particular interest is its contrasting distribution with the Dog Rose. It rarely extends into regions receiving more than 40" of rain yearly, in distinction to the Dog Rose which is by far the most abundant canine rose. In the British Isles then, the generally higher rainfall restricts the distribution of sweet brier largely because of competition from other plants. In New Zealand the prevalence of large areas receiving less than 40" of rain yearly restricts the distribution of the Dog Rose, again probably through competition from better adapted species.

Since the migration of European peoples began several centuries ago, sweet brier has extended its range considerably. It is widespread in eastern and western North America as a plant of roadsides, waste places, and neglected pastures (Rehder, 1940), and is known from Argentina (Parodi, 1959) in the Andean foothil zone. It has been recorded in every state in Australia except the Northern Territory, but it is in New Zealand

that it reaches a level of abundance which is unsurpassed by any other country. As Dr. R. Melville, Royal Botanic Gardens, Kew, once remarked to me, "there are probably more plants of sweet brier within a radius of 30 miles from Alexandra, Central Otago, than there are in the whole of the British Isles".

312. Distribution in New Zealand

Sweet brier is distributed almost throughout New Zealand. In 1916 the Board of Agriculture sent out circulars to farmers and Field Inspectors of the Department of Agriculture asking for information on noxious weeds. Sweet brier was included in 94 out of 328 replies from the South Island, and in fewer than 20 out of 341 replies from the North Island.

A survey by the Department of Agriculture in 1954-55 found that sweet brier occurred in every county in the South Island except Fiord county, and was scattered throughout the North Island except in Taranaki and the Central Plateau. The latest survey in 1961-62 by the same organisation found that its distribution extended to every county in New Zealand except Fiord county.

In the North Island it occurs rather sporadically, and although it is locally abundant in the eastern provinces, it is not generally considered a serious pest on pastoral land. In the South Island it is concentrated in tussock grasslands east of the Main Divide. The largest populations occur in Marlborough, Canterbury, and Otago. They usually form large tracts of mixed thorny scrub which are linked by smaller communities of pure or mixed scrub and numerous, scattered individuals.

The fact that many of these large populations are directly related to past or present habitations such as mining settlements, shepherd's and rabbitier's huts, coach stables, homesteads, etc., suggest that man was the principal agent in its initial dispersal.

313. Altitudinal and other limitations

Sweet brier is essentially a plant of low altitudes, and in the South Island it is found from sea-level to the uppermost limit of short-tussock grassland, which varies between 2,500 ft and 4,000 ft depending on latitude and local aspect. This is also the climatic upper limit of all introduced and many indigenous shrub species.

Like many shrubs with weedy tendencies, whether introduced or native to this country, it is not a serious problem in sown pastures, and it tends to be restricted to disturbed ground or where the indigenous vegetation has been modified or devastated by the activities of man. These sites have several features in common:

- (1) The vegetation is nearly always open and competition is negligible.
- (2) Soils are naturally fertile, immature, or rejuvenated. Thus the level of fertility is high.
- (3) Soils are usually well drained and aerated.
- (4) Grazing is invariably light or confined to other, more palatable species.

Such conditions are ideal for colonising shrubs like sweet brier. Its distribution and density, therefore, are closely related to the

frequency of these conditions.

In low-rainfall areas, as in Central Otago and parts of Marlborough, the natural level of soil fertility is relatively high and competition from other plants has been negligible in the past. Sweet brier is widely distributed in these areas and its density is controlled more by soil moisture and by the frequency and intensity of grazing.

Another factor is rapidly becoming more important. At one time rabbits were numerous in these areas, and the indigenous vegetation was degraded to its lowest form, while vast areas were almost completely denuded. Few plants of sweet brier could establish under these conditions, and those present before the rabbit were uniformly grazed. Since 1950, with a spectacular reduction in rabbit numbers, there has been an increase in the density of sweet brier. However, a simultaneous regeneration of competitive plants, especially grasses, seems to have partly filled this ecological "vacuum" which sweet brier briefly exploited. There is strong field evidence that grass competition is the limiting factor in the further spread of sweet brier, more especially on darker, moister aspects and more mature soils.

Under medium and high rainfall conditions, particularly in Canterbury, soils in their natural state are weakly weathered, strongly leached, and relatively infertile. With increasing rainfall there is a corresponding increase in grasses, other herbs, and heath-like shrubs, all of which will tolerate low fertility and compete strongly for nutrients in short supply. The main factors limiting the spread and density of sweet brier in these areas seem to be soil fertility and plant competition. Thus it is restricted to recently formed, immature soils, or to rejuvenated mature

soils. The former include young alluvial fans, river beds, rock outcrops, and loose stony debris; the latter, all manner of eroded soils, chiefly on steeper slopes with a northerly aspect. These sites again are well drained but well watered, seasonally flushed with nutrients, sparsely covered with vegetation, and tend to be undergrazed.

Sweet brier, like most oportunist plants, seems to grow where it can. It has a definite climatic upper limit, but the fact that it grows on a certain soil type or on a particular aspect merely indicates part of its range. It does not necessarily follow that those sites are the best for growth and reproduction. As in England, it will grow on soils derived from weathered limestone (rendzina soils), but it is not restricted to them, nor does it achieve its maximum density or performance on them. I believe that the so-called "calcicolous" status of sweet brier (cf. Salisbury, 1952; Tansley, 1939) is a misinterpretation of the habitat conditions found in the chalk grasslands of S.E. England. They approach the conditions found in drier parts of the South Island in almost every respect, namely weak competition, high fertility, good drainage and aeration, and a chronic history of rabbit deprecation.

Sweet brier comes in close contact with many shrubland and grassland species, native and introduced, because of its wide distribution and ecological amplitude. It also borders the principal forest communities, ranging from subtropical podocarp-broadleaf forest in the north, to subantarctic beech forest in the south. As such, a list of species associated with sweet brier would serve a doubtful purpose. It is proposed, therefore, to discuss typical examples of vegetation found within the limits of abundant sweet brier in the South Island. This vegetation is confined to the rainfall shadow, east of the Main Divide.

321. Forest communities

Sweet brier seldom enters continuous forest or even dense woodland since it is essentially a plant of open habitats. I have not observed it in the principal beech forests which flank the Main Divide, nor does it appear in the podocarp-broadleaf or mixed beech-podocarp forests of the eastern foothills. Several features of forest habitats prevent its entry and maintenance.

- (1) Poor conditions for germination (731).
- (2) Poor conditions for seedling growth (Chapter 5) such as low light intensity, generally over-moist and infertile soils, and competition from other plants in the field layer and forest understory.

However, sweet brier plants may be found either within or on the margins of secondary forest of varied composition and ecological status (figures 3,1 and 3,2). In general these communities are small in extent and scattered in their distribution. As a rule they are young, most of

Fig. 3,1.

Beech forest remnant (Nothofagus solandri var. cliffortioides) on the dark brier site at Flock Hill. Note the dense carpet of tutu (Coriaria sarmentosa) around the forest margin, and the scattered shrubs of sweet brier at the forest edge.

Fig. 3,2.

Beech forest remnant (Nothofagus solandri var. cliffortioides) on the sunny brier site at Flock Hill. Note the fragmentation of the forest, and the dense scrub of sweet brier and other species penetrating into the forest clearings.



them post-dating the wholesale destruction of primary forest begun by Polynesian burning within the last 1,000 years. Although they vary floristically and structurally, they tend to be more open than undisturbed forest, and the understory and field layer are weakly developed. In addition, the soils are rejuvenated and often fairly fertile.

These conditions allow entry of sweet brier, largely from seed carried by birds, opossums, and deer. A few seedlings will survive and maintain themselves in "light pools" and just inside the forest edge, but most are weak stemmed, and their reproductive capacity is retarded. The chief factors operating against its success are low light intensity accompanied by cool and moist soil conditions.

Nevertheless, sweet brier demonstrates its ability to exploit any gap in the forest floor or canopy, particularly in eastern areas where the forests are drier and floristically impoverished in comparison with their counterparts in wetter regions. It seems to fill a gap where we would expect to find indigenous understory shrubs, though it barely qualifies as a significant stage in forest succession.

322. Shrubland communities

Within the climatic range of sweet brier in the South Island there are three principal types of shrubland, each with its floristic, physiognomic, and ecological features.

- (1) Shrubland dominated by introduced plants such as gorse (Ulex europeus) and broom (Cytisus scoparius).

- (2) Shrubland dominated by heath-like plants such as manuka (Leptospermum scoparium), kanuka (L. ericoides), and cassinia (Cassinia fulvida).
- (3) Shrubland dominated by a range of shrubs with generally a spiny or divaricate growth habit (e.g., Discaria, Coprosma, Corokia, Olearia), and a preference for open habitats.

Both gorse and broom will form impenetrable thickets which develop rapidly into a one-layered and almost monospecific scrub community. The former usually colonises abandoned or derelict pastures on relatively stable hill soils, and in wetter areas will be invaded by broadleaf scrub forest species - the forerunners of true forest. The latter is most common on bouldery river terraces and may be regarded as a pseudo-climax community. Because of their gregariousness and rapid growth, both species prevent invasion from other shrubs. Sweet brier may enter into the composition of both communities where the terrain is more broken, but it is usually found around the edges with other half-shade species. In a few instances, particularly on riverbed terraces, sweet brier was the initial coloniser, but it has since lost its dominance to broom, hawthorn (Crataegus oxyacantha) and elderberry (Sambucus nigra). The essential feature of such scrub is its predominant introduced character, and only a few native shrubs are found in the community.

The second type of shrubland is essentially indigenous in composition, though it too can display the same weedy propensities as introduced scrub. Manuka and cassinia usually occur on infertile soils in moister regions as seral communities during the development of scrub forest and true forest. Where the soils are stable, the field layer is usually dense, and sweet

brier is unable to enter or maintain itself. Where the soils have been laid bare or rejuvenated by erosion, the shrubs are more dispersed, the field layer is absent or negligible, and sweet brier usually gains entry. A mixed community of heath-like, thorny, and unarmed shrubs develops slowly and unevenly. It may reach a pseudo-climax as mixed scrub, or it may be invaded by true forest species. On the other hand, it may be converted to thorny, thicket scrub by burning and accelerated erosion, thus favouring sweet brier.

Shrubland dominated by kanuka extends into drier regions on more fertile soils where it may be open and dispersed, permitting the entry of thorny shrubs such as sweet brier or, under moister conditions, it may form dense scrub which has all the appearances of low forest, and excludes most other shrubs.

The third type of shrubland is by far the most abundant and widespread, colonising a great variety of soils, but usually those that are young or rejuvenated, fertile, and free draining. The ubiquity and abundance of this scrub is due largely to the spine-bearing and divaricate habit of most of the species, and the fact that the fruits are dispersed by birds. Some unarmed species such as Olearia and Corokia are often interspersed. The scrub has a mixed composition and no one species dominates, except for matagouri (Discaria toumatou) which can form one-layered thickets that are sometimes invaded by true forest species. The field layer is extremely diverse, containing survivors of grassland and open habitats, and forerunners of scrub and true forest (figures 3,3 and 3,4).

Sweet brier will enter into the composition of such scrub but will not dominate it unless it is burnt, in which case an almost pure community

Fig. 3,3.

Types of plant communities. Secondary beech forest at the summit with a zone of Dracophyllum scrub below it on the hillslopes. The large fan in the centre consists of an older portion covered in short-tussock grassland, and a rejuvenated portion to the left carrying mixed thorny scrub dominated by matagouri (Discaria toumatou) and sweet brier.

Fig. 3,4.

Mixed thorny scrub on a rejuvenated hill soil at Dry Creek. The dominant shrubs are sweet brier, matagouri, Coprosma propinqua, and corokia cotoneaster.



of sweet brier will emerge because of its power of regeneration after fire, and its faster growth rate. The mixed thorny scrub which is again essentially indigenous, is the closest approximation we have to the thorn scrub thickets of Europe which sweet brier and other wild roses will enter as primary colonisers.

323. Grassland communities

As noted earlier (313), sweet brier does not invade sown grassland, nor does it enter arable land or permanent hill pastures composed mainly of English grasses and/or legumes. Dense native grassland in wetter climates is poorly colonised by sweet brier and is generally hostile to establishment of most other shrubs.

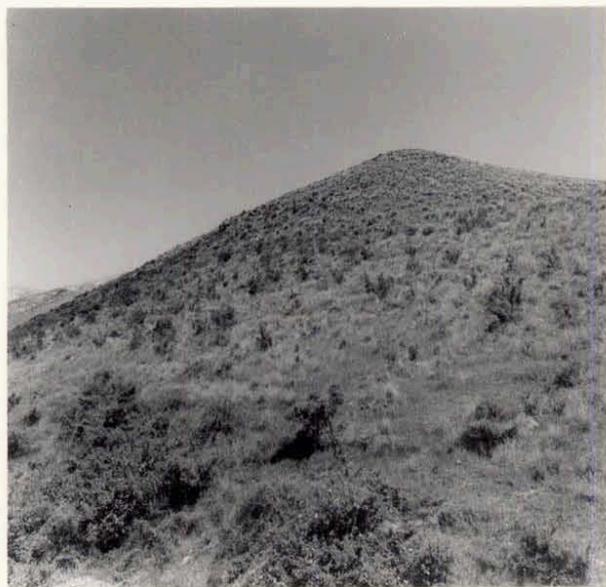
Sweet brier is essentially a coloniser of degraded grassland, especially the short-tussock grasslands of the eastern South Island, which have a chronic history of exploitation and mismanagement. A large part of this grassland itself represents a retrogressive stage in succession following forest destruction in Polynesian times. Although it grows on a variety of soils and in a wide range of climate, this grassland is noted for its floristic poverty and the ease with which it is transformed or destroyed. On flat and rolling land in moister regions, it has been successfully invaded by sward-forming grasses such as browntop and sweet vernal to the exclusion of most other herbs, least of all shrubs. On steeper land in the same regions, and on all terrain in drier regions, the life conditions and competitive relations of the habitat are more delicately balanced. When this balance is upset, usually by overgrazing, burning, or both, the grassland becomes depleted to the extent that

Fig. 3,5.

Dense grassland dominated by browntop (Agrostis tenuis) and sweet vernal (Anthoxanthum odoratum) in the Cardrona Valley, showing the distribution of sweet brier in the moister depressions on the hillslopes, and at the break in slope, and its restricted distribution on the adjacent flats.

Fig. 3,6.

Short-tussock grassland (Festuca-Poa) on the rejuvenated hill soil at Dry Creek, with scattered plants of sweet brier.



indigenous colonisers and introduced annuals prevail.

Apart from matagouri, Hymenanchera alpina, and minor sub-shrubs, there are very few native or introduced shrubs which will colonise degraded tussock grassland as rapidly and effectively as sweet brier (figures 3,5 and 3,6). It owes part of its ability to establish in these habitats to its possession of prickles as well as to the edaphic and biotic suitability of the site. But the important factor controlling its colonisation is the management to which the grassland is subjected.

324. Sweet brier in open habitats

It has already been mentioned that sweet brier will invade forest, scrub, or grassland, gaining entry where these communities are open and the field layer or sward is thin and discontinuous. Sweet brier also establishes readily in crevices and rock outcrops and loose, stony debris throughout the tussock grassland environment. At present it is a familiar plant on steep eroding hill sides, rocky gullies, roadcuts, riverbed alluvium, and raw colluvial fans. In each case it is accompanied by survivors or forerunners of scrub and grassland. It is also found in a variety of man-made open habitats associated with gold mining, such as sluice deposits, dredge tailings, and even the stone walls of derelict huts. The seed is freely dispersed by birds, and once the plants become established they grow rapidly in these open habitats in the virtual absence of competition other than their own shade and demand for root space. They become very robust and arborescent, and reproduce freely. (figures 3,7 and 3,8).

51a

Fig. 3,7.

Robust plants of sweet brier occupying the eroding
embankment of a roadcut at Dry Creek.

Fig. 3,8.

Steep, rocky slopes near Cora Lynn, covered with
thick scrub of sweet brier and matagouri.



325. Miscellaneous associations

Sweet brier is a common plant of roadsides in the South Island, and its ubiquity in this habitat reflects the absence of animal grazing and general neglect. As a rule these sites are fairly fertile due to past disturbance, and are often well watered by continual runoff. Although competition can be fierce, sweet brier usually gains entry at some early stage or when the vegetation is opened up through burning or clearing (figure 3,9).

Hedgerows are another familiar habitat for sweet brier (figure 3,10). Gorse and broom hedgerows are nothing more than lines of artificial scrub which are frequently colonised by other shrubs. However, pure hedges of sweet brier are rare.

Railway embankments, waste places, derelict quarries, and the edge of water races are other favoured habitats of this ubiquitous shrub. All these sites provide the edaphic requirements and partial release from intense land use favoured by colonising shrubs.

329

Fig. 3,9.

The roadside habitat in the Cardrona Valley, showing the continuous ribbon of robust sweet brier plants.

Fig. 3,10.

A typical gorse hedge (Ulex europeus) in Canterbury, with an emergent plant of sweet brier.



CHAPTER 4

STRUCTURE, LIFE HISTORY, AND SEASONAL BEHAVIOUR

INTRODUCTION

This chapter is concerned with the structural and behavioural aspects of sweet brier which are determined largely by its genetic constitution. It aims to provide a basis for later discussion of the effect of environmental variations. Observations were carried out on plant material in the Waimakariri catchment and at Lincoln, except where stated otherwise. The information deals with N type sweet brier and A type features are introduced solely for comparison. Attention is drawn also to certain abnormal characteristics of special interest which, as far as can be judged, are genetically determined.

SECTION 1. THE SEED AND EMBRYO411. Flowering and seed development

Flower primordia are initiated during the growth of terminal and axillary buds of the previous-season's vegetative and flowering shoots. Buds in the upper region of these shoots produce flowers while the lowermost ones remain dormant, or if activated, vegetative (421). The approximate time of flower initiation was determined by examining buds at frequent intervals from the onset of winter dormancy. In 1961 and 1962 bud growth began about mid-August and the first flower primordia were observed four weeks later when the first and second leaves of the flowering shoot had unfolded and the lamina of the third (usually the largest) was partly unfolded. Five weeks later young flower buds 1.5 mm long could be felt between the upper leaves, but were not yet visible. Buds eventually appeared and progressed to the

"pink-bud" stage during the next four to five weeks. Meiosis apparently occurs in the anthers of Rosa when the buds appear between the stipules of the subtending scale leaves (Erlanson, 1930).

The first of the monoclinous flowers opened at Lincoln on 18 November 1962 and one week later at Cora Lynn, the warmest field site. In the Waimakariri catchment, flowering reached a peak in the second and third weeks of December, and had almost ceased by the first week in January. Flowers may open at any time during the day, though predominantly overnight. For flowers opening overnight at Lincoln the anthokinetic cycle was determined as follows (observations were made at 4 p.m. each day).

- 1st Day: Sepals spreading; petals bright pink, slightly recurved; stamens yellow, recurved over stigmatic dome, anthers dehisced but no pollen shed; stigmas pale green, arranged in compact dome, dry and unreceptive.
- 2nd Day: Sepals reflexed; petals bleached, fully expanded; stamens spread away from stigmatic dome, some pollen shed; stigmas fully protruded, arranged in loosely compacted dome, sticky and receptive, a few pollen grains adhering but no germination.
- 3rd Day: Sepals reflexed; petals bleached, falling; stamens light yellowish brown, recurved over stigmatic dome; stigmas light yellowish brown, sticky, encrusted with pollen, many grains germinating.
- 4th Day: Sepals reflexed; petal fall complete; stamens yellow brown, completely obscuring stigmatic dome; stigmas light brown, drying out, pollen tubes observed in stigmatic tissue.

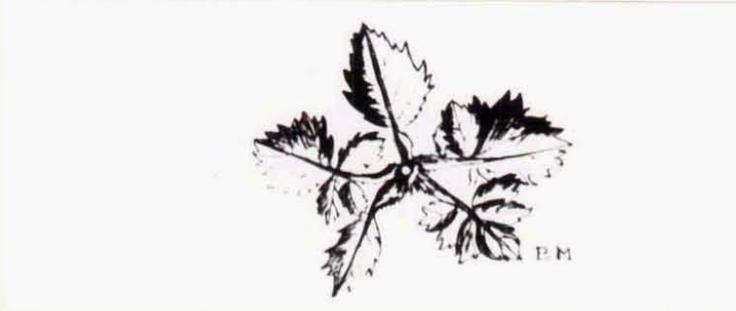
Fig. 4,1.

Teratological phenomena in sweet brier.

Proliferous flower on elongated, heavily armed peduncle. Normal fruit to right. (c. $\frac{1}{2}$ natural size).

The same enlarged, showing median floral proliferation and foliaceous sepals (x3).

Sepal phyllody. Calyx in adaxial view (x2).



10th Day: Sepals spreading to sub-erect; stamens and stigmas brown, dry, withered; fruit visibly swelling.

The actual stage of fertilization was not observed, but the evidence above together with the experimental data on the breeding system (214) suggests that it occurs within six days of anthesis.

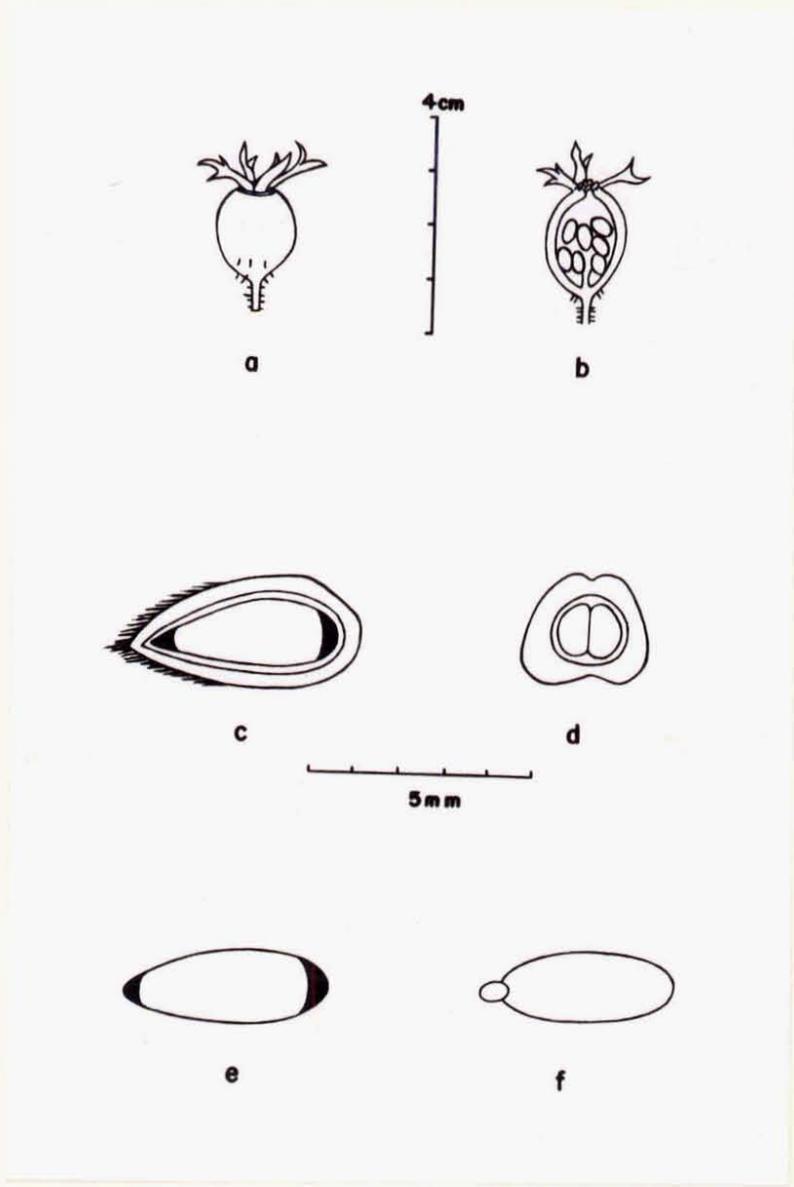
Usually only one crop of flowers is produced each season, though a few flowers may appear in late autumn. These usually result from abnormal growth of the first bud behind the apex of the new-season's flowering shoot. Late flowers are associated also with teratological phenomena which arise during the reproductive phase. Teratomata such as proliferous flowers and foliaceous sepals were not infrequently recorded (figure 4, 1), and the condition is common in Rosaceae (Masters, 1869; Bond, 1945) and in many other families. The causal agent often is unknown, though in Rubus idaeus (Bos, 1957) the abnormalities are clearly associated with a virus-induced witches' broom disease "dwerz ziekte". Late flowers, though normal structurally, rarely set seed. Most fail to ripen before the onset of frost, the contents degenerate, and the still-green fruit withers and drops.

The ripe "fruit" is a red fleshy "hip" enclosing the achenes or true fruits which are cream coloured, hard and bony, and bearing a tuft of bristles at the styler end. Encased within is the seed with its tough brown skin or testa. The seed is exalbuminous, consisting of two white cotyledons and a white bud-like embryo (figure 4, 2). Plants grown outside at Lincoln set seed in their third season, but in nature the age of plants at first seed set may be much greater

Fig. 4,2.

Fruit of sweet brier.

- a. normal hip with persistent sepals.
- b. sectioned hip.
- c. achene cut longitudinally, showing the thick pericarp and seed in central cavity.
- d. achene cut transversely, showing the two cotyledons.
- e. seed enclosed by the testa.
- f. seed with testa removed, showing the embryo and one cotyledon.



(5 - 10 years or more). During the summer of 1961/62 the development of "single" fruits on one plant at Flock Hill was recorded. Peak flowering here was over by 20 December and at anthesis the hip was small (c. 8mm long) and green, and the unfertilized ovules - the potential achenes - were already 2.5 - 3mm long. Table 4, 1 shows volume increase of the hip, and length growth of achenes, cotyledons, and embryo.

Table 4.1. Development of fruit at Flock Hill 1961/62.

<u>Date</u>	<u>22/12</u>	<u>4/1</u>	<u>19/1</u>	<u>7/2</u>
Vol. of hip (ml)	0.48 \pm .09	1.10 \pm .08	1.25 \pm .14	1.24 \pm .11
Length of achene (mm)	3.90 \pm .40	4.60 \pm .24	4.70 \pm .40	4.70 \pm .26
Length of cotyledons (mm)		0.47 \pm .05	1.78 \pm .20	2.66 \pm .07
Length of embryo (mm)		0.24 \pm .04	0.49 \pm .04	0.61 \pm .04

The hip and achene developed steadily until 19 January, but after that no significant changes occurred. Length growth of the cotyledons and embryo ceased almost three weeks later. The hip changed from green to a faint reddish brown by 7 February and the flesh was firm and moist. At first the achene was pale green, easily punctured with a dissecting needle, and the pericarp tissue was moist, but by 7 February it was cream coloured, punctured only with firm pressure, and the pericarp tissue was drying out. The contents of the achene were transparent and gelatinous on 26 December, whereas on 7 February the cotyledons and embryo almost completely filled the cavity, and the tissues were opaque, moist, and jellylike. During February the hip turns yellow then orange, and in March adopts its characteristic red coloration.

The hip flesh breaks down in April, and in May the hip is wrinkled, soft, and jammy. By August it is somewhat pendulous, reddish black and drying out. Hips sometimes fall or are cropped by animals within twelve months of their formation. However, it is common to find one- and two-year-old hips still attached to plants. At Omarama, four-year-old hips were seen on several plants.

Not all the ovules reach fruitfulness, and the number of achenes per hip varies with environment (632). Studies of seed also revealed the occurrence of split and extra cotyledons (pleiocotyly); a condition apparently not infrequent in polyploids and one which has been associated with a state of imbalance of the chromosomes (Haskell, 1954). In seedlings reared at Lincoln tricotylys predominated over split cotyledons, but subsequent dissection of many seed lots showed that the frequency of occurrence in any year was very low.

Table 4.2. Percentage frequency of tricotylys in two forms of sweet brier (All seed 1961/62 crop. N = 200).

<u>Type</u>	<u>N</u>	<u>A</u>
Dry Creek	2.0	3.0
Flock Hill	1.0	3.0
Lake Pearson	1.5	3.5
Cora Lynn	1.0	1.0

A further 24 samples of N type seed from the same sites were examined in conjunction with other tests, and the frequency of tricotylys ranged from 0.5 to 3%. In the achene the three cotyledons occur as discrete organs, though it is not known whether they split during ontogeny or developed independently from separate rudiments. The growth of pleiocotylyous seedlings is discussed in Section 2 (421).

412. Water content of ripe seed.

Hips were collected from Flock Hill throughout the 1961 season to determine the water content of achenes at different stages of hip development. Following each harvest the achenes were removed from the hips, cleaned of extraneous matter and two samples of 200 oven-dried at 100-105°C.

Table 4.3. Mean percentage water content of achenes during 1961.

<u>Date</u>	<u>6/2</u>	<u>13/3</u>	<u>11/5</u>	<u>16/8</u>	<u>19/10</u>	<u>6/12</u>
Hip colour	green	orange	red	red	dk. red	red/black
Hip texture	firm	firm	soft	jammy	soft	leathery
Water content of achenes	32.7	27.6	25.0	23.9	20.6	18.6

The progressive loss of water can be accounted for by the maturation of seed and the drying out of the pericarp and hip flesh. A direct measurement of the water content of seed was not practicable since it requires considerable skill to remove the pericarp without damaging the contents. However, by air-drying the achenes, thus removing water from the pericarp, a reasonable estimate of the water content of seed should be obtained. This was demonstrated initially by selecting a batch of achenes harvested on 24 July 1961, when the hips were moist and jammy, and air-drying for 60 days prior to treatment (weights are averages per achene).

<u>Weight before treatment</u>	<u>Weight after treatment</u>	<u>% water content</u>
19.6 mgm	17.3 mgm	11.7

Additional samples from the same harvest were stored in open containers at room temperature for two years. After one year the water content dropped to 7.9%, after two years, 6%. These results compare favourably with those obtained for air-dried achenes from several South Island localities (632). Because of this low water content seed stored under these conditions for several years remains in a viable state (415). Such low percentages were not encountered in the field where the pericarp rarely dries out completely, though achenes retained on plants for extensive periods are almost in an air-dry condition. Samples of 1960 and 1961 achenes were collected from plants at Flock Hill on 19 August 1962, and the average percentage water contents were 11.2 and 11.4 respectively.

Achenes harvested on 16 August 1961 and air-dried for 30 days failed to imbibe after steeping in distilled water for periods of up to 90 days. Similar tests on achenes air-dried for longer periods at room temperature and naturally in the field had the opposite effect. Samples stored at room temperature for two years and with a water content of 6% were either fully submerged in open containers (A), or sown on moistened filter paper in covered petri dishes (B).

Table 4.4. Uptake of water by air-dried achenes.

Treatment	Mean weight (mgm)		Mean water content (%)	
	A	B	A	B
Before treatment	17.1	17.5	(6)	(6)
24 hrs. "	20.7	21.3	27.1	27.3
7 Days "	21.6	22.1	32.2	32.6
14 " "	21.5	22.2	31.6	33.1
24 " "	21.5	22.2	31.6	33.1

The achenes thus imbibed water rapidly during the first 24 hours. Treatment differences were not significant. These figures are comparable with those obtained for achenes stored outside in soil at Lincoln (414).

413. Viability

In this subsection achene production and the potential germinative capacity of seeds are discussed. The distinction is here made between the capacity of a seed to germinate - usually determined by a rapid viability test - and actual germination which is discussed in the following subsection (414).

Sweet brier produces hips in ample quantities each year irrespective of a wide range of site conditions, though on excessively drained sites in semi-arid areas the physiological condition of plants may be such that hip primordia abort during development. Achene production, on the other hand, is extremely variable. According to Fagerlind (1951), 100% achene production occurs in Rosa rubiginosa L. after self pollination or pollination with a number of canine roses. However, it has already been noted (411) that in nature all the potential achenes do not usually develop. Generally, the hip contents can be separated into three distinct classes: fully developed achenes, underdeveloped achenes of intermediate and miniature sizes which are assumed to result from the degeneration of fertilized products at different stages of development, and undeveloped and presumably non-fertilized primordia.

The proportion of achenes in each class varies according to the type of brier, within plants, from one locality to another, and from year to year under natural conditions of pollination (632). Table 4,5 illustrates the mean achene production in "single" hips at Lake Pearson where adverse environmental conditions seldom pertain. It also compares both types of brier at this site.

Table 4,5. Mean achene production of single hips of sweet brier. N = 100 hips. Provenance = Lake Pearson 1961 crop.

Type of brier	Fully developed achenes	Underdeveloped achenes	Undeveloped achenes	Total potential
N	23.1 \pm 4.9	0.7 \pm 1.1	7.6 \pm 4.4	31.4 \pm 3.9
A	6.1 \pm 3.7	2.3 \pm 2.0	23.4 \pm 6.7	31.8 \pm 5.0

A large proportion of potential achenes in N type brier are not fertilized and a small number of seeds degenerate during development. In A type brier, the proportion of achenes in the main classes is reversed due to a high degree of pollen sterility (214). There is also a higher incidence of seed degeneration.

Hips borne in corymbs are usually larger than those borne singly, and within each corymb the uppermost hip (terminal) is noticeably larger than the rest (lateral). As Table 4,6 shows, there is a close relationship between hip size and achene production.

Table 4,6. Mean achene production in terminal and lateral hips of N type brier corymbs. N = 100 hips. Provenance = Lake Pearson 1961 crop.

	Fully developed achenes	Underdeveloped achenes	Undeveloped achenes	Total potential
Terminal hips	35.1 \pm 4.7	0.80 \pm 0.92	14.2 \pm 2.4	50.1 \pm 3.5
Lateral hips	29.1 \pm 3.3	0.70 \pm 0.66	8.1 \pm 3.7	37.9 \pm 2.2
S.E. of diff.	1.83	0.29	1.40	1.82
P	<0.01	0.8-0.7	<0.01	<0.01

The potential for achene production is significantly higher in terminal than in lateral hips, but a greater proportion of ovules are not fertilized. Nevertheless, more fully developed achenes are produced per hip.

The quality of fully developed achenes also varies. Very often the embryos degenerate, and although the achenes appear normal, the contents are black and shrunken. Larvae of the rose seed chalcid, Megastigmus aculeatus, may also consume the entire contents of normal achenes and reduce the quantity of sound seed (711). Thus, standard laboratory tests have proved unsatisfactory for determining the germinative capacity of brier seed, and since seedlings are produced erratically over a number of years from samples sown outside (414), a quicker method for predicting the germinative behaviour was desirable.

The excised embryo technique perfected by Flemion (1948) is reliable and accurate, but requires considerable skill and is very time-consuming. Some workers have used the "flotation test" for rose seed, but with mixed results. Another method commonly used is to

dissect the achenes and count the number of plump and presumably viable seeds. However, such methods are based on rather tenuous assumptions and not on germination itself or even factors correlated with germination, and the results are not absolutely reliable. A more direct method is the topographical staining technique developed by Lakon (1949). Properly prepared seeds are placed in a colourless solution of a tetrazolium salt (in this study 2,3,5 - triphenyl tetrazolium bromide - T.T.B.). In live seeds, the colourless solution is reduced by dehydrogenase activity to a red formazan which stains the seeds, but the enzymes are absent from dead tissues which remain unstained (figure 4,3). The technique is simple, and by applying the correct interpretation of the colour reaction, a rapid estimate of seed viability is obtained (see appendix 4,1). The last three methods are compared in Table 4,7. In the main part of the table, each batch of achenes is divided according to the flotation test and subdivided after an examination of their contents. Dissection and T.T.B. tests were carried out on separate samples, each of 100 achenes. The percentage viability was calculated from the number of seeds which sank in the flotation test; from the number of plump seeds in the dissection test; and from the staining pattern in the T.T.B. test.

Fig. 4,3.

Typical tetrazolium staining patterns in sweet brier seeds. Adequately stained tissue shaded black, weakly stained stippled, no stain clear. The carved side is always unstained. Classes a and b only are considered viable.

Fig. 4,4.

Seedling emergence from N type seed at Lincoln 1962-63. n = 400 seeds. Provenance = Lake Pearson 1961 crop.

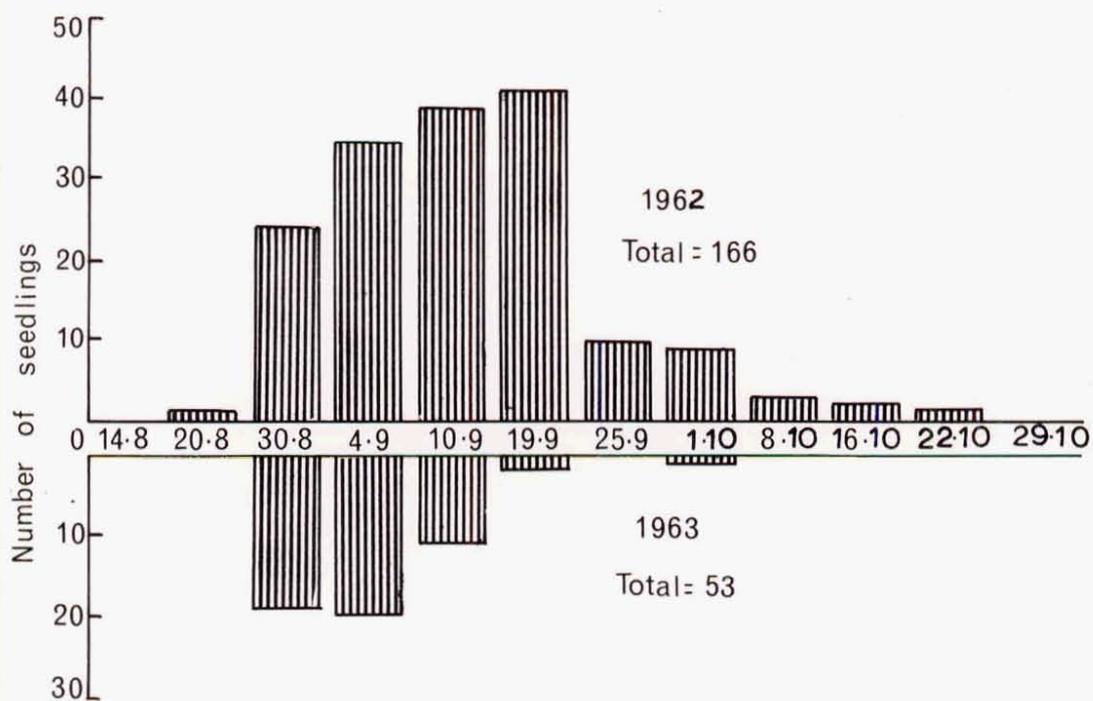
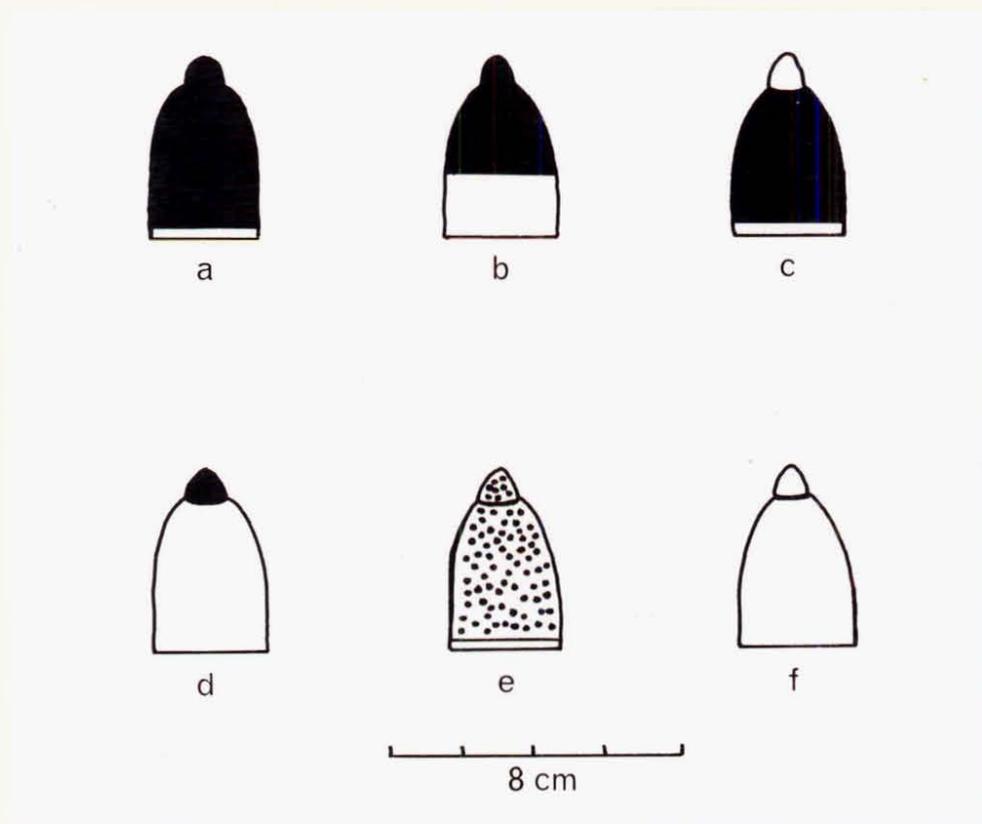


Table 4,7. Comparison of flotation, dissection, and T.T.B. viability tests on sweet brier seed (fully developed achenes >2 mm diameter, 1961 crop).

Locality Site	Dry Creek 3,600 ft.	Dry Creek 2,500 ft.	Flock Hill shaded	Flock Hill sunny	Contents of achene
Type of brier	N	A	N	N	
Floated	32	42	2	12	shrunken
	64	26	48	16	plump
	0	8	0	0	larval damage
Sank	0	0	0	9	shrunken
	4	10	50	361	plump
	0	14	0	2	larval damage
Viability %					
Flotation	4	24	50	93	
Dissection	68	36	98	94	
T.T.B.	81	60	94	97	

These results show the T.T.B. test to be the most and the flotation test the least reliable of the methods tried. There is a close agreement between all three for seed harvested from favourable sites, but in shaded habitats and at high altitudes, the fertilized contents are poorly developed and consequently do not fill the entire cavity. Similarly, in A type brier secondary degeneration of seeds is common giving rise to malformed contents in otherwise normal achenes. Under these conditions the flotation and dissection methods tend to underestimate viability. Properly applied, the T.T.B. test eliminates all errors due to laboratory technique, and observer differences are reduced to a minimum. The test has proved invaluable for tree and shrub seeds which require long germination test periods (Grabe and

Delouche, 1959).

In N type brier a high percentage of fully developed achenes may have viable seeds as the data from Flock Hill indicate (table 4,7). Conversely, seeds of A type brier have mostly low viability. This is supported by the results of T.T.B. tests on samples from the achene production study at Lake Pearson (tables 4,5 and 4,6).

Table 4,8. Percentage viability of seed of single hips.
N = 200 fully developed achenes.
Provenance = Lake Pearson 1961 crop.

Type of brier -----	Aborted or non-staining -----	Infested with Chalcid larvae -----	Viable seeds -----
N	8.5	9.0	82.5
A	24.5	21.5	54.0

The actual number of sound seeds in N type brier is relatively high, and if parasitism is excluded, then the potential viability is much higher still. In A type brier, low viability is related to a higher incidence of seed degeneration and a heavier infestation of chalcid larvae. The mean number of seeds per hip capable of germinating is 19 and 3 respectively for N and A type brier at this site.

T.T.B. tests were also carried out in connection with studies of seed development to determine at what stage the test could be applied. Reliable results were obtained as early as the beginning of February when the hips were green and firm.

414. Germination

Freshly harvested sweet brier seed, after four weeks' prechilling, gave 1% germination in 49 days and 9% in 451 days when tested at the Government Seed Testing Station. Germination under natural conditions takes place during a limited period in spring from seed which has been in the soil for at least one year. This is in line with the so-called deep dormancy which is characteristic of many rosaceous seeds (Crocker and Barton, 1931).

Dormancy in Rosa varies with species or hybrid (Rowley, 1956), and in addition the depth of dormancy may be modified by environmental conditions during seed development (Von Abrams and Hand, 1956).

Factors believed to condition dormancy in Rosa include:

- (a) physiological reactions in the embryo necessitating a period of post-harvest low temperature after-ripening to bring about prompt and complete germination (Crocker and Barton, 1931; Tincker, 1935).
- (b) mechanical barriers to water imbibition such as the impervious inner seed coat (Asen and Larson, 1951).
- (c) physical restriction imposed by the pericarp (Jackson and Blundell, 1963).
- (d) growth and germination inhibitors contained in the achene (Jackson and Blundell, 1963).

The limited amount of work done on seeds of R. rubiginosa has shown them to be very sensitive in the time and temperature required for breaking dormancy (Barton, in litt., 1959). They give excellent

germination in soil in the greenhouse after six months in moist sand at 5°C. Lower and higher temperatures (1° and 10°) and shorter periods at 5° are ineffective. A search of the literature fails to reveal other references to the germination of this species.

The main emphasis in this study was placed on the quantitative aspects of dormancy. Also, it was important to determine the extent to which seeds designated viable emerged as seedlings.

The germination procedure was as follows: After harvesting, the achenes were removed from hips, cleaned, and riddled through appropriate sieves to separate the various achene classes. A large sample (approximate population sample) of fully developed achenes was thoroughly mixed, and two working samples of 400 achenes were withdrawn by the system of quartering. One was put aside for a T.T.B. test, while the other was dusted with a commercial seed sterilant and sown one inch deep in potting soil in shallow flats. The soil surface was covered with a film of fine stone chips to prevent moss growth, and the flats were embedded in a sawdust mulch outside at Lincoln. The flats were examined frequently and seedlings pricked out as they appeared. Successful emergence was credited when the hypocotyl and cotyledons appeared above the soil surface irrespective of the normality or vigour of the seedling.

Two methods of expressing results were adopted:

- (a) "Apparent emergence", or the number of emergent seedlings expressed as a percentage of the original seed lot.
- (b) "True emergence", or the number of emergent seedlings expressed as a percentage of the viable seeds in the original seed lot.

The viability of sown samples is assumed to be close to the viability of corresponding test samples, and this assumption was shown to be reasonably valid provided the population sample was thoroughly mixed. It is certain, however, that some of the original viability is lost during soil storage. Also, some seeds may germinate but fail to emerge. Therefore, the figures presented are to some extent approximations to the true position.

A typical pattern of seedling emergence is shown in Table 4,9. In this instance seed was harvested from Lake Pearson on 30 June 1961 and sown on 15 July 1961.

Table 4,9. Cumulative percentage emergence of sweet brier seedlings. N = 400 seeds. Provenance = Lake Pearson 1961 crop.

Type of brier	1961		1962		1963		Population viability % (T.T.B.)
	Apparent	True	Apparent	True	Apparent	True	
N	0.2	0.3	41.5	49.1	54.7	64.8	84.5
A	0.2	0.3	15.2	29.6	17.5	34.0	51.5

The viability of both types of brier is evidently not expressed by the number of emergent seedlings. A little more than half the N type and about one sixth of the A type seeds had produced seedlings by the third season, and the majority of these emerged during the second season. Only two seedlings emerged in 1964, one in each treatment. This trend is exhibited also by the closely related Rosa canina (Rowley, 1956).

At Lincoln, seedling emergence begins in mid-August, extending over a period of about two months, though most seedlings appear during the first three to four weeks (figure 4,4.). The periodicity of

emergence is remarkably uniform both at Lincoln and in the natural environment, and there is a close relationship between the time of emergence and bud break on overwintering shoots.

Some attention was given to the variability in emergence among different seed lots.

The first comparison involves seed from three plants at Flock Hill. The seed was harvested on 24 July 1961, and sown one week later. No seedlings emerged in the first spring after sowing, and none emerged in 1964.

Table 4,10. Cumulative percentage emergence of seedlings from seed of separate N type plants.
N = 400 seeds. Provenance = Flock Hill 1961 crop.

<u>Plant Number</u>	<u>1962</u>		<u>1963</u>		<u>Sample viability % (T.T.B.)</u>
	<u>Apparent</u>	<u>True</u>	<u>Apparent</u>	<u>True</u>	
1	7.0	7.3	10.2	10.7	95.5
2	11.7	12.1	13.5	13.9	97.2
3	14.0	15.2	17.7	19.2	92.2

Seeds from these plants varied in their ability to produce seedlings, and the overall low percentage is an unaccountably poor expression of the sample viability.

Rowley (1956) found that seeds from terminal hips of R. canina do not germinate differently from those from lateral hips. Tests with sweet brier showed a similar periodicity of emergence among seed of terminal and lateral hips, though slightly more seedlings emerged from seed of the former which are noted for their larger size and higher seed set. Again, no seedlings emerged in the first spring after sowing, and none emerged in 1964.

Table 4,11. Cumulative percentage emergence of seedlings from seed of terminal and lateral hips of N type plants. N = 400 seeds. Provenance = Flock Hill 1961 crop.

<u>Hip type</u>	1962		1963		Sample viability % (T.T.B.)
	<u>Apparent</u>	<u>True</u>	<u>Apparent</u>	<u>True</u>	
Terminal	14.5	18.1	23.7	32.8	80.0
Lateral	12.0	14.3	21.2	25.3	84.0

The age of the seed, or, more probably, the conditions of storage, was found to have a pronounced effect on the speed of emergence and the total number of seedlings produced. Seed produced in 1960 at Dry Creek was harvested on 29 May 1960, cleaned, and stored in paper containers at room temperature. Seed produced in the same year was harvested one year later on 9 June 1961, along with seed produced in that year also. Samples from all three harvests were sown on 20 June 1961. No seedlings emerged in the first spring after planting, and only one emerged in 1964.

Table 4,12. Cumulative percentage emergence of seedlings from N type seed of different ages and storage. N = 400 seeds. Provenance = Dry Creek 1961 crop.

<u>Year of production</u>	<u>Date of harvest</u>	1962		1963		Sample Viability % (T.T.B.)
		<u>Apparent</u>	<u>True</u>	<u>Apparent</u>	<u>True</u>	
1960	29.5.60	57.0	63.9	65.0	72.9	89.2
1960	9.6.61	36.0	41.1	38.3	42.7	89.7
1961	9.6.61	30.7	49.8	32.0	51.8	61.7

Since the potential germinative capacity of the 1960 harvests is about the same, differences in emergence are possibly explained by the effects of storage on tissues external to the embryo. It is well known that dry storage affects the permeability of seed coats (Barton, 1961).

The low total emergence of the 1961 harvest is complicated by environmental factors. 1961 was a poor year for seed production at Dry Creek. Partial drought conditions resulted in a high degree of secondary seed abortion, hence the low viability.

The third and final comparison involves seed lots from the same population sample of N type plants. These were sown on 15 August 1961, seven days after harvesting.

Table 4,13. Cumulative percentage emergence of seedlings from different seed lots of the same population sample.
N = 600 seeds. Provenance = Lake Pearson 1961 crop.

Lot number	1962		1963		Population viability % (T.T.B.)
	Apparent	True	Apparent	True	
1	33.8	35.4	52.5	55.0	93.2
2	29.3	30.7	43.8	45.9	"
3	28.2	29.5	39.0	40.8	"
4	30.3	31.8	35.3	37.0	"

Individual seed lots varied in their ability to produce seedlings, and the range in both total apparent and true emergence exceeded 17%. A few more seedlings emerged in 1964, raising the total apparent figures to 57.0 and 35.5% for lots 1 and 4 respectively, and increasing the range to 22.5%. Once again viability was not expressed by the number of emergent seedlings.

To summarise, a few seeds of sweet brier will germinate in the first spring following their production, provided they are effectively buried beforehand, but peak germination always occurs in the second spring - a feature of "two-year species" (Barton, 1961). It is apparent that immaturity in the embryo is not the cause of dormancy in

Rosa; nor do the testa and pericarp of some Rosa spp. prevent access of water to the embryo (Jackson and Blundell, 1963). It is likely, as these authors suggest, that seeds of sweet brier require a long period of burial which favours the decay of the mechanically restrictive pericarp, or the leaching out of growth inhibiting substances from the seed coats, or both.

Germination under experimental conditions and in nature is erratic extending over several years, and although the potential germinative capacity as determined by vital staining of live tissues may be high, it bears little relation to the total number of seedlings produced. That final germination is closely related to seasonal fluctuations in external factors, particularly temperature, is suggested by the limited period in spring during which it occurs, the poor results usually achieved under laboratory conditions, and the uniform periodicity from year to year at any one site. If we also consider the variation in germination between different seed lots together with variations due to the environment in which the seed is produced (632), the difficulties in providing a full explanation become apparent.

415. Longevity

Very little is known about the life span of rose seeds.

Ewart (1908) tested the germination of sixteen seeds of R. rubiginosa var. latifolia after 50 years of dry storage with negative results.

Other "vintage" rose seed in his experiments behaved similarly.

However, the ability of R. rubiginosa seeds to withstand dry storage for shorter periods has been reported by Crocker and Barton (1931) who obtained 23.8% germination in nineteen months from seed held at room temperature for three years. Degeneration under these conditions is apparently very slow, probably, as Barton (1961) suggests, because the seeds have their metabolic processes greatly reduced.

Short-term retention of viability under artificial storage conditions is shown by results obtained in the present study in which seed of N type plants was stored dry in various containers, or moist in river-washed sand at different temperatures.

Table 4,14. Effect of artificial storage on the viability of sweet brier seed. N = 200 seeds. Provenance = Lake Pearson 1961 crop.

Conditions of storage	Mean temperature (°C.)			No. years stored	Viability % (T.T.B.)
	Max.	Min.	Mn.		
Control				nil	78.0
Room (1)	+26.0	+13.0	+19.5		
Corked phial				1	75.5
" "	+27.0	+14.0	+20.5	2	78.5
Uncorked "	+26.0	+13.0	+19.5	1	75.5
" "	+27.0	+14.0	+20.5	2	83.5
Seed packet	+26.0	+13.0	+19.5	1	77.5
Moist sand				1	78.5
Room (2)	+22.2	+20.0	+21.1		
Petri dish				1	77.5
Moist sand				1	78.0
Refrigerator (1)	+ 6.1	+ 4.7	+ 5.4		
Petri dish				1	76.5
Moist sand				1	82.5
Refrigerator (2)	-12.2	-20.0	-16.1		
Corked phial				1	77.5
Uncorked "				1	78.0

A more important aspect is the effect of natural storage conditions on seed viability. Tests were carried out on seed of N type plants stored on the soil surface and buried at different depths at Lincoln. In one test, seed and hips harvested from Dry Creek on 9 June 1961 were sown on the surface and buried one inch deep in standard potting soil in shallow flats for one year. Prior to germination, samples of each were recovered for viability and moisture determinations.

Table 4,15. Percentage viability and moisture content of seed after one-year's soil storage. N = 200 seeds. Provenance = Dry Creek 1961 crop.

Conditions of storage -----	Sample viability (T.T.B.)		Mean moisture content % -----
	Before treatment -----	After treatment -----	
Surface hips	69.2	30.0	17.4
Buried hips	69.2	59.5	27.8
Surface seed	71.7	17.5	16.0
Buried seed	71.7	65.8	34.0

Loss of viability occurred in all treatments, with significant reductions in all seed stored on the soil surface, probably due to extremes of temperature and frequent wetting and drying. Loss of viability in the soil was most likely caused by rotting due to water and micro-organisms. The effects of burial on seed moisture contents and subsequent seedling emergence are further illustrated in Figure 4,5.

In another test the condition and behaviour of buried seed was determined over a longer period. Provision was made for two years' storage, and lots of 500 seeds were stratified at depths of 1, 2, 4 and 8 in. in standard potting soil in porous clay pots. The pots were set in the ground so that the soil surface inside the pot was level with that outside. The study site was at Lincoln, and rainfall totals for the storage periods 1961-62 and 1962-63 were 28.3 and 28.0 in. respectively.

After the first year's storage the number of seedlings which emerged in each treatment was counted.

Fig. 4,5.

Seedling emergence in 1962 from seed stored on and below the soil surface. Provenance = Dry Creek 1960 crop.

- | | |
|-----------------|-----------------|
| 1. surface hips | 2. buried hips |
| 3. buried seed | 4. surface seed |

Fig. 4,6.

Germination and early seedling growth.

All except a are drawn to the same scale.

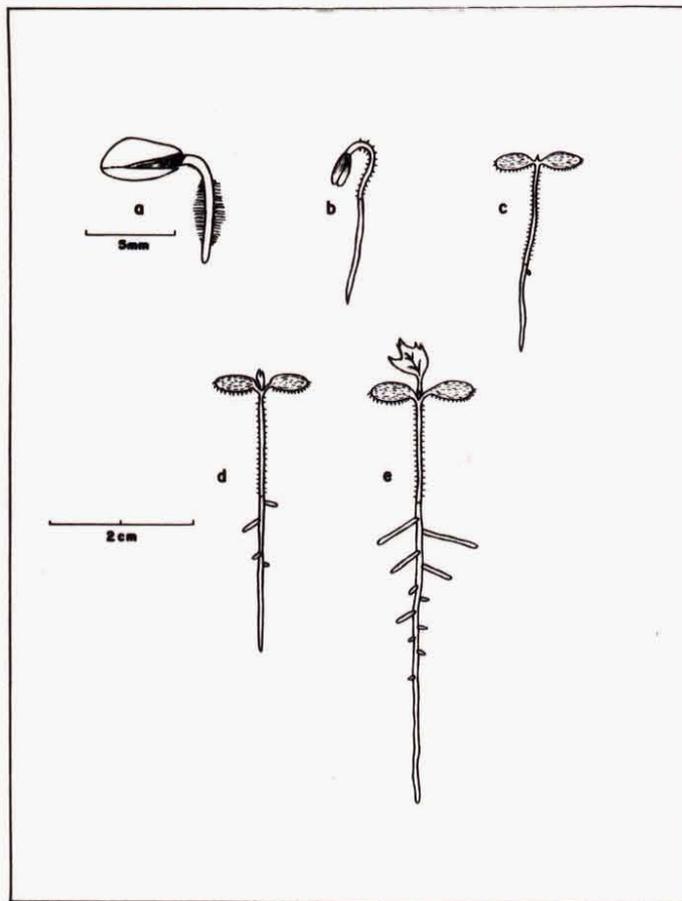
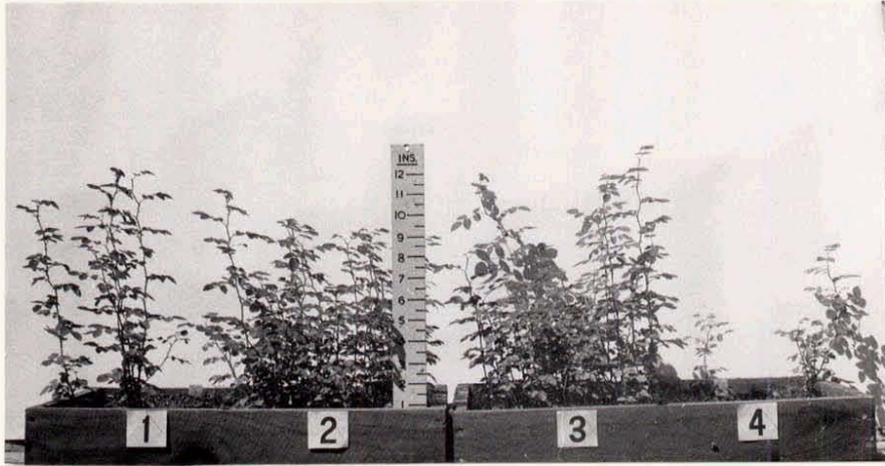


Table 4,16. Percentage apparent emergence of seedlings from seed buried at four depths for one year. N = 500 seeds. Provenance = Lake Pearson 1961 crop. Viability (T.T.B.) before treatment = 78%.

<u>Length of treatment</u>	<u>Depth of burial</u>	<u>1 in.</u>	<u>2 in.</u>	<u>4 in.</u>	<u>8 in.</u>
1 year		56.8	7.6	-	-
2 year		41.6	5.4	-	-

Thus, deeply planted seed failed to produce seedlings and most of those which emerged from the 2 in. depth arose around the edge of the pots. When emergence had ceased, pots in the one-year treatment were lifted and all remaining seeds were washed out and examined. A number of seeds buried at 2 in. had actually germinated, but apart from those situated near the edge of the pot, most failed to emerge. It appears that the physical stress exerted by the covering soil was the main inhibiting factor. A few seeds also had germinated at 4 in., but no germination occurred at 8 in., probably due to a reduction in intensity of the requisite stimuli.

It was not possible to separate primary rotted seed from those which germinated but failed to emerge, and the two were grouped as one category - non-emerged seed. The remaining whole seed was then subjected to a T.T.B. test. Table 4,17 summarises all the data concerning seed buried for one year.

Table 4,17. Fate of sweet brier seed after one-year's storage at different depths in soil. N = 500 seeds. Provenance = Lake Pearson 1961 crop. Viability (T.T.B.) before treatment = 78%.

Depth of burial	Apparent emergence %	Non-emerged seed %	Remaining whole seed %	Viability of remaining whole seed %
1 in.	56.8	28.4	14.8	33.7
2 in.	7.6	46.4	46.0	32.5
4 in.	-	35.6	64.4	21.5
8 in.	-	26.0	74.0	20.5

An obvious effect is the significant loss of viability of non-germinated seed. Shallow burial favours germination and emergence, but it also leads to a high percentage of seed rotting. The same procedure was repeated after two-years' storage.

Table 4,18. Fate of sweet brier seed after two-years' storage at different depths in soil. N = 500 seeds. Provenance = Lake Pearson 1961 crop. Viability (T.T.B.) before treatment = 78%.

Depth of burial	Cumulative emergence %		Non-emerged seed %	Remaining whole seed %	Viability of remaining whole seed %
	1 yr.	2 yr.			
1 in.	41.6	55.4	38.0	6.6	6.6
2 in.	5.4	6.0	61.8	32.2	6.2
4 in.	-	-	46.6	53.4	15.3
8 in.	-	-	59.6	40.4	22.2

After two-years' storage most of the seed buried at 1 in. either germinated or rotted. At 2 in., although some germination occurred, seedling emergence was restricted and many seeds rotted. At 4 and 8 in. germination was retarded and about half the original seed lots rotted. The viability of the remaining whole seed at all depths was very considerably reduced.

416. Discussion

Sweet brier produces one set of flowers each year from primordia initiated during the new-season's growth of flowering shoots. Under experimental conditions, plants begin to flower in their third season, but in nature flowering begins later still. Given average site conditions, abundant flowering can be expected over a period of about four weeks. Although insect pollination does occur, selfing is common, and the species is facultatively self-fertilizing (214). This ensures satisfactory seed set each year. After fertilization seeds develop rapidly, maturing on the plant in a fleshy torus or hip. In the cold winter months of June and July, when normal forage for animals is in short supply, the hips are red, soft and jammy, and very attractive as an alternate food source. By this time the seed is fully developed and well protected by the tough bony pericarp, enabling some seed to pass through the animal digestive tract in a viable state. Thus, a large percentage of newly-ripened seed is cropped and dispersed principally by birds and mammals. Others after-ripen on plants in almost an air-dry condition for 1-3 (-4) years. These, however, take little part in the dispersal of the species.

The viability or potential germinative capacity of freshly harvested ripe seed is very high, often exceeding 80% of a sample of fully developed achenes. But this figure far exceeds the number of seeds which actually germinate. Germination itself is erratic, extending over several years, and seeds do not germinate until the second spring following their production. There appears to be no uniform physiological behaviour underlying germination, though recent

work suggests that both mechanical restriction and growth inhibiting substances are involved. The possession of innate seed dormancy - a feature of many rosaceous plants - should act as a stabilising influence on sweet brier populations in the face of adverse site conditions. Also, from the viewpoint of weed control, it should prevent isolated acts of eradication from having any permanent effect. It does appear, however, that the life of seed in the soil is very short. Experimental evidence indicates that while shallow burial favours germination, it also hastens seed decay and loss of viability. Germination is severely retarded in seed lying on the soil surface or buried at depths greater than 2 in. In all cases involving seed storage in the soil, the viability of non-germinated seed was significantly reduced after two years. It would be interesting to test the behaviour of seed stored in a wide range of soils and rainfall regimes.

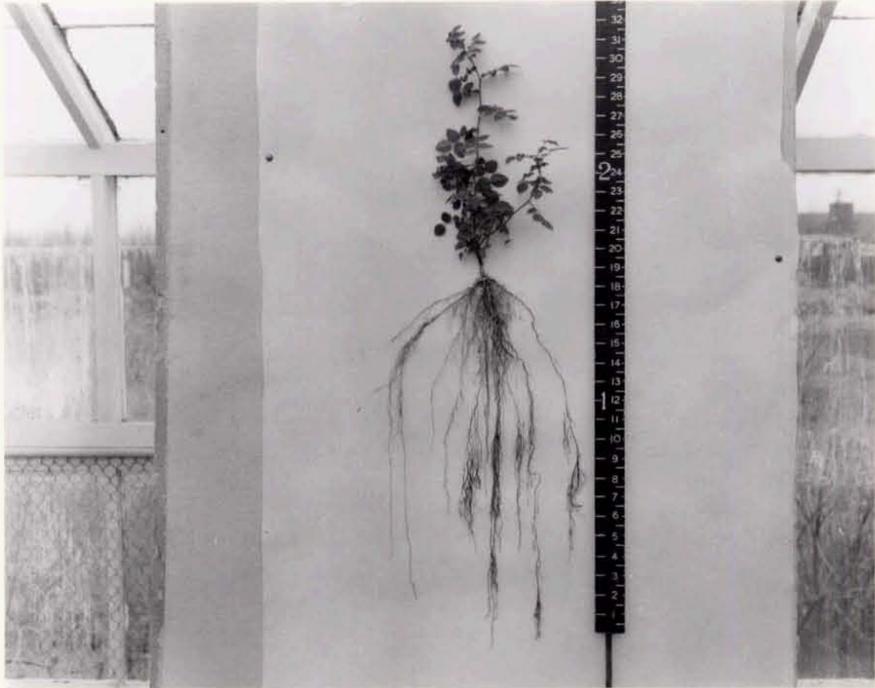
SECTION 2. THE SHOOT AND LEAVES421.

In germinating, the seed visibly swells forcing apart the pericarp at the radicle end along the line of suture. The testa ruptures and the radicle protrudes and penetrates the soil (figure 4,6). Then the hypocotyl elongates forcing the seeds towards the soil surface. As the cotyledons expand, the testa is ruptured further and finally shed. At this stage the hypocotyl is 4-6 mm long, and the cotyledons 3-4 mm long, yellow and pressed together, enclosing the minute stem apex. Prior to emergence, the hypocotyl is 10-15 mm long, and the cotyledons about 4-5 mm long and pale yellow with a faint greenish tinge towards the base. When the cotyledons are half expanded, the hypocotyl reaches its full length of 20-25 mm. By this time the first leaf is barely visible as a minute projection of the enlarged terminal bud. Later stages up to the expansion of the first leaf are shown in Figure 4,6. Seeds with protruding radicles were placed in moist soil in an unheated greenhouse on 26 November 1962, and seedlings reached the two-leaf stage on 24 December. In the early stages of seedling development, the hypocotyl is fleshy and turgid, pink above the soil surface, and bears clear stalked glands. The cotyledons are also fleshy; green and eglandular on the upper surface, and pink and glandular below and on the margins. Later, the hypocotyl becomes brown and woody, and the cotyledons turn yellow and fall.

First-year seedlings grown in an unheated greenhouse in 1962 had by the end of the summer developed leafy main shoots up to 40 cm long, and shorter side shoots and basal shoots up to 20 cm long originating from the lowermost axillary buds of main stems (figure 4,7). Plants of the same age grown under supra-optimal conditions (542) were more

Fig. 4,7.

First-year seedling grown in the unheated
greenhouse.

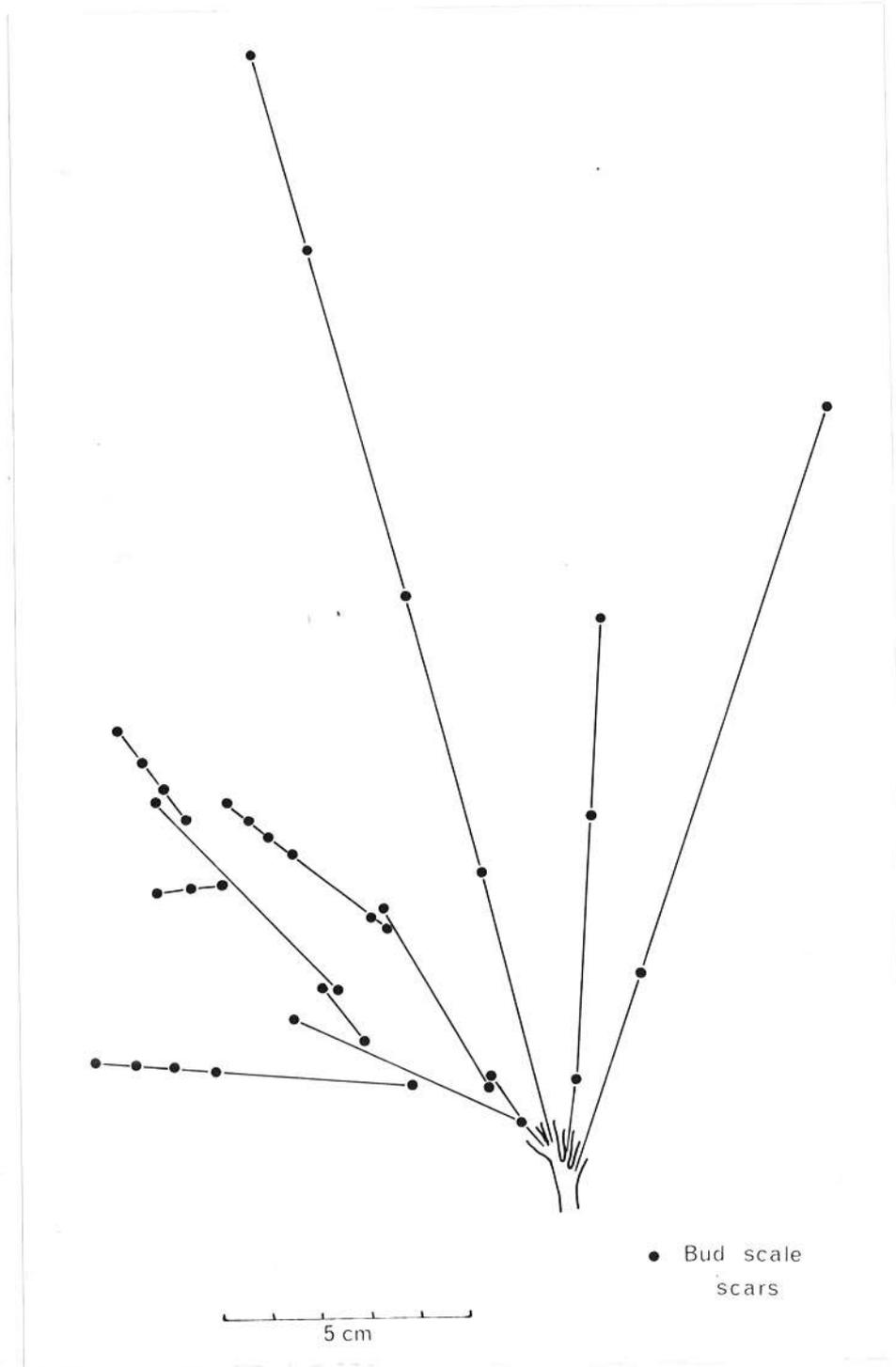


robust, consisting of main stems with basal shoots and numerous side shoots. Growth of second-year seedlings in the greenhouse results in a short extension of one-year-old shoots and the outgrowth of axillary buds into shorter side shoots. At the same time, rapid growth of new basal shoots and underground stems begins. Thus, by the end of the second season, plants possess 1-3 upright basal shoots - the first-year fruiting canes of mature plants; a weaker, straggling "juvenile" shoot system; and one or more underground stems. In nature, even under optimal conditions, the appearance of the first fruiting canes is delayed, and plants may remain in the juvenile state for 7 or more years (figure 4,8). Under sub-optimal conditions, plants may retain a monaxial habit for even longer periods. One single-stemmed plant 12.5 cm long, consisting of a series of short internodes and numerous leaf scars, was 14 years old.

The early growth of seedlings reared from fully developed and under-developed achenes was compared. Several grams each of miniature and intermediate achenes - the two underdeveloped classes - were sown in 1961 in connection with the main germination experiments. One miniature seed germinated in 1962, but its cotyledons were very small, distinctly chlorotic, and the seedling withered and died. Twenty seven intermediate seeds also germinated in 1962, and of these, 13 had very small, malformed or chlorotic cotyledons, and later died. The remaining 14, though small, appeared normal and healthy. Ten of these together with ten seedlings from fully developed achenes of the same provenance were planted in deep double flats. The flats were placed in an unheated greenhouse on 4 October 1962 and watered at regular intervals. On 4 January 1963, when the "fully developed" seedlings

Fig. 4,8.

Schematic diagram of a typical wild seedling with its juvenile shoot system. The actual plant was 7 years old.



showed some signs of soil exhaustion, both lots were harvested and measured.

Table 4,19. Growth of first-year seedlings derived from under-developed and fully developed achenes.
N = 10 seedlings. Provenance = Lake Pearson 1961 crop.

<u>Achene category</u>	<u>Mean main stem length (cm)</u>	<u>Mean number secondary stems</u>	<u>Mean total stem length (cm)</u>
Under-developed	22.8 ± 3.3	4.0 ± 1.7	36.4 ± 10.0
Fully developed	34.5 ± 2.5	7.1 ± 1.5	86.7 ± 11.6
S.E. of diff.	1.30	0.72	4.87
P	<0.01	<0.01	<0.01

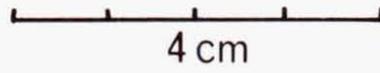
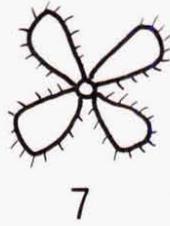
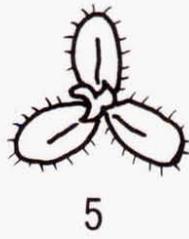
Seedlings reared from under-developed achenes were smaller in all their parts, with smaller leaves, shorter internodes, and fewer side shoots. In the critical phase of establishment, such small seedlings with a limited food reserve are more likely to be eliminated.

A further comparison concerns the early growth of pleiocotylous seedlings. Various forms of pleiocotyly were observed among newly emerged seedlings of N type brier. These ranged from abnormal, almost monocotylous seedlings to equi-angled tetracotylous seedlings, but tricotylys were more prevalent (figure 4,9). Several examples of each form were planted in porous clay pots, placed in an unheated greenhouse, and their growth habits were observed. Seedlings with abnormal and split cotyledons generally were slow growing, lacked vigour, and were inclined to be bushy. Tricotylys varied in total height, leaf shape and extent of bushiness. Some remained monaxial - one with almost distichous leaves - others were very bushy (figure 4,10), while a few remained small and closely resembled some A type progeny in all their parts. Despite these variations, there appeared to be no radical

Fig. 4,9.

Pleiocotyly in sweet brier.

1. dicotyl
2. abnormal monocotyl
3. pseudo-tricotyl
4. tricotyl
5. equi-angled tricotyl
6. pseudo-tetracotyl
7. tetracotyl



departure from the phyllotaxy and shoot arrangement met with in sweet brier. It is concluded that such variations are due, as Haskell (1954) suggests, to chromosomal imbalance of the polyploid parent plants.

The mature sweet brier plant consists of a long-lived stool or crown which supports a dense colony of arching, perennial shoots or canes. The shoot has a determinate type of growth, and branching is definite or cymose. The external appearance of undisturbed plants is that of a shrub to aborescent shrub.

Shoots arise in four different ways (figure 4,11):

1. as stem suckers (basal shoots, replacement shoots, water sprouts, bottom breaks) from dormant or adventitious crown buds.
2. as lateral branches from dormant buds above ground level. These are divided into (a) lateral branches from axillary buds in the lower half of mature shoots, and (b) lateral branches from supernumerary buds much higher up. The former are more vigorous than the latter.
3. as stem suckers from dormant buds of subterranean stems.
and more rarely
4. as root suckers from adventitious buds in the proximal region of major roots which have been exposed.

The pattern of shoot growth is similar to that in many other roses. Stem suckers arise annually, enlarging the colony of mature shoots and replacing old or injured ones. They begin to grow before mature shoots come into flower. Others may appear at somewhat later intervals. Growth at first consists of the enlargement and bursting of crown or trunk buds, and the appearance of the young shoot of which

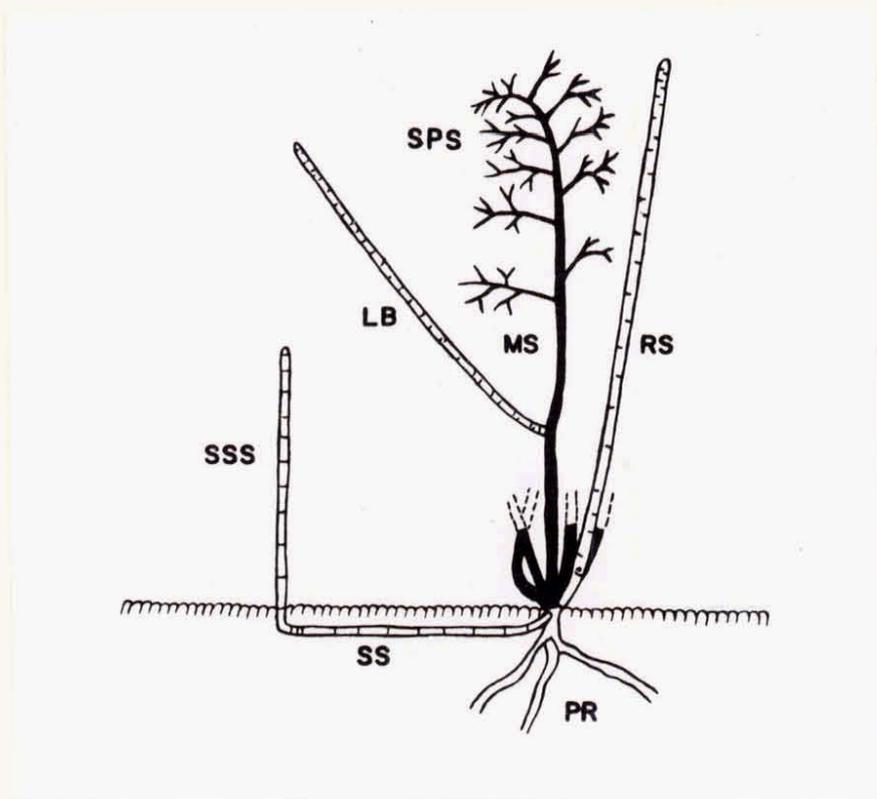
Fig. 4,10.

Growth habit of two types of tricotyloous seedlings.

Fig. 4,11.

Schematic diagram of the shoot system of mature plants.

- MS. mature shoot or cane
- RS. basal or replacement shoot
- LB. lateral branch
- SPS. spur shoots
- SS. subterranean stem
- SSS. subterranean stem sucker
- PR. parent roots



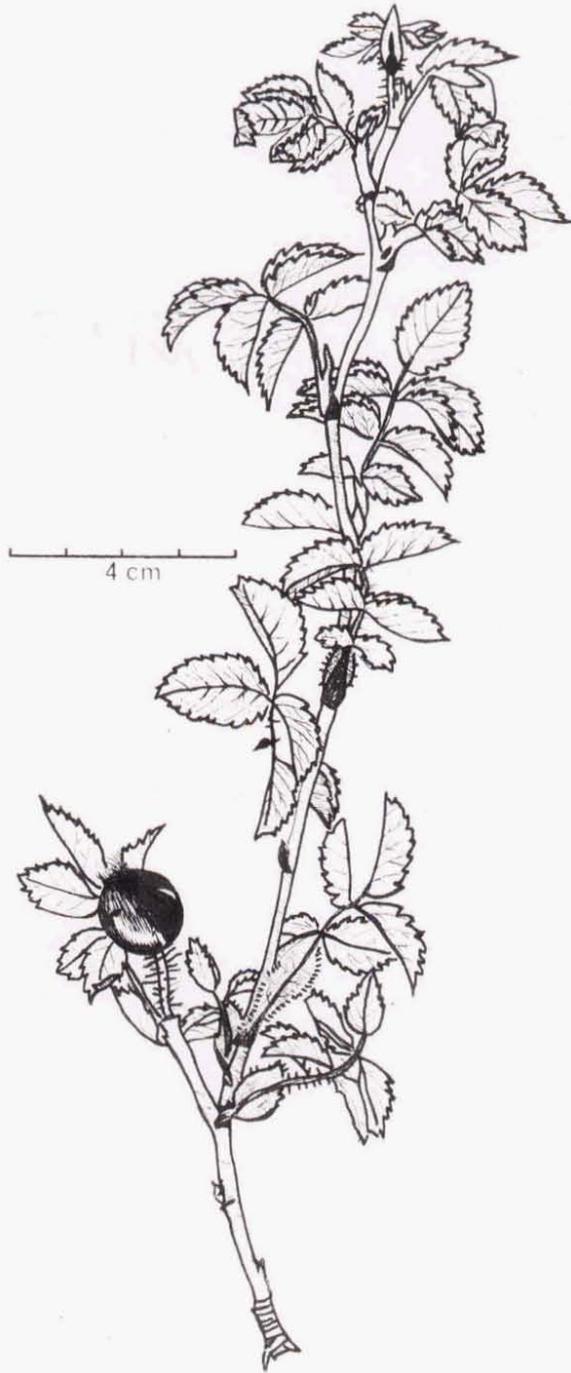
the apical meristem initiates leaf primordia. The growing point, protected by young sheathing leaves, is carried upwards by rapid elongation of the proximal internodes, and a long (2 - 3 m), leafy, unbranched shoot is formed. Towards the end of the growing season, extension growth ceases and a terminal resting bud is formed. The young shoot is at first vigorous, highly pigmented, and succulent, but gradually it becomes lignified. When extension growth ceases it consists of a series of nodes (60 - 80 (-100)) and internodes, and the entire shoot is prickly, glabrous, and photosynthetic. In the following season, buds in the upper half of the shoot extend into leafy, fruiting laterals. As these flower, other leafy laterals (spur shoots) are produced from the first large axillary bud behind the flowering apex (figure 4,12). This pattern is repeated in subsequent years resulting in a bushy cane which increases in diameter and ceases to be photosynthetic (figure 4,11).

A similar pattern of development is shown by vigorous lateral branches and root suckers.

Subterranean stems are the chief means of vegetative extension. They originate from dormant or adventitious buds in the undifferentiated region between roots and shoots, usually just below ground level, and begin to grow about the same time as stem suckers. Compared with the latter, they are much slower growing, smaller in diameter, non-photosynthetic, and less pigmented. The leaves are reduced to scales and the armature to a sparse cover of fine bristles. Shoots arising in this manner may renew extension growth each season for a number of years without sending up suckers. Thin, woody shoots rooting at the

Fig. 4,12.

Typical flowering shoot of sweet brier, with a vigorous non-flowering lateral produced in the same season from the first axillary bud behind the flower apex.



nodes and as old as 6 - 10 years were traced several metres from parent colonies. At this stage they probably act as functional roots. It appears that physical soil conditions rather than a uniform endogenous mechanism is responsible for the eventual emergence of subterranean stem suckers in undisturbed colonies. If the colonies are disturbed, however, both basal shoots and subterranean stem suckers are induced to grow. The latter arise from terminal or axillary buds, usually in the distal region of subterranean stems, and their growth pattern is similar to that of normal stem suckers, but they are smaller in all their parts. In subsequent years a new colony is formed and remains connected to the parent colony indefinitely.

In healthy, undisturbed colonies, shoots in the canopy of mature canes appear to suppress dormant crown and basal stem buds, probably by hormonal control. With the onset of flowering, or when the mature canes lack vigour and begin to die, this suppression is released and replacement shoots form at the base of the colony. In the canopy itself the uppermost spur shoots suppress dormant buds on the lowermost side of the cane, probably also by hormonal control. This gives the mature cane its typical asymmetric branching habit.

The number and size of replacement shoots is associated with plant vigour. The chief contributing factors are bright sunlight, moderate temperature, high humidity, optimum soil water and adequate nutrients. Nitrogen is widely regarded as a key nutrient for production of replacement shoots in cultivated roses. When lacking, the number of shoots is reduced.

There is no information on the longevity of sweet brier plants, though some canine roses in Europe are reputed to be several hundred years old (Willmott, 1911). It is not uncommon to find living canes 20 - 25 years old on New Zealand material. However, the precise ageing of veteran plants is practically impossible because of their multiaxial growth habit. It is certain, however, that veteran plants in established populations are older than 50 years.

The first leaf of sweet brier seedlings is unifoliate, but successive leaves are more complex (figure 4,13). The full compliment of seven leaflets is attained at the twelfth node on the main stems of vigorous seedlings grown in the greenhouse. On the other hand, leaves of suppressed seedlings may not progress beyond the trifoliate stage for several years. A similar gradation in leaf shape, leaflet number and size is common to all new shoots whether vegetative or flowering. But the largest leaves of one-year-old stem suckers are much longer (\pm 12 cm) than those of flowering shoots (\pm 6 cm). The leaflets are fairly uniform in structure possessing unicellular hairs on the upper surface, and stalked capitate glands below. In leaves grown in full sunlight there are two distinct layers of pallisade perenchyma, and stomata are situated on the lower surface.

Fig. 4,13.

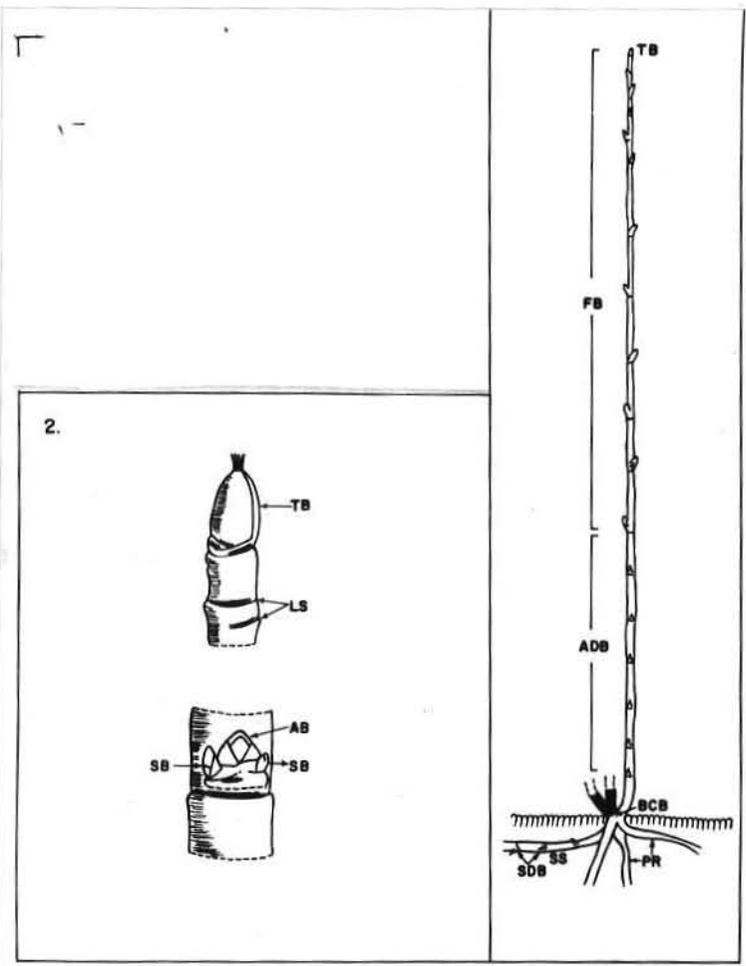
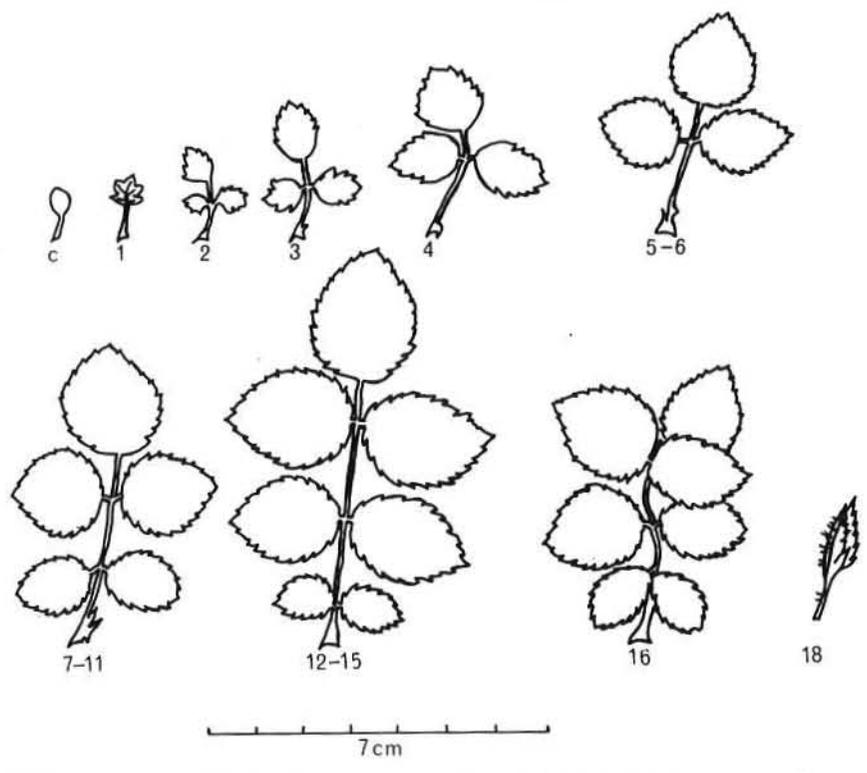
Successive leaves from a first-year seedling grown in the unheated greenhouse. The 18th leaf has not yet expanded. c = cotyledon.

Fig. 4,14.

Types of bud in sweet brier.

- TB. terminal bud
- AB. axillary bud
- SB. supernumerary bud
- FB. fruit bud region
- ADB. aerial dormant bud region
- BCB. basal crown bud region
- SDB. subterranean stem
- SS. subterranean stem
- PR. parent roots
- LS. leaf scars

(diagrammatic, not to scale).



SECTION 3. SEASONAL ACTIVITY OF BUDS431. Field observations

Overwintering buds of sweet brier vary in size and shape with the type of shoot on which they occur and their position on these shoots. On all mature shoots there are terminal or apical buds, lateral buds axillary to foliage leaves, and supernumerary buds axillary to bud scales (figure 4,14). Axillary buds are further divided into inflorescence (upper), and aerial dormant (lower) buds (figure 4,14).

Apical buds of spur shoots are about 5-10 mm long and uniform in structure. Many are axillary buds which have assumed a terminal position after a shoot has flowered. Each bud consists of the following organs (figure 4,15):

- (1) Two outer scales with petiolar portions only, enclosing the bud at its base, together with two supernumerary buds 0.36 - 0.50 mm long.
- (2) Two inner scales consisting of a petiolar portion with the lamina reduced to a pencil of hairs.
- (3) Three or four innermost scales with prominent petiolar and rudimentary lamina portions. These ensheath the young bud.
- (4) An apex of 6 - 8 foliage leaf primordia with prominent lamina portions. The oldest is about 1 mm long.

All outer scales are glandular on the margins, somewhat dry, and stained with anthocyanin. Inner scales are glandular and clothed with clear, epidermal hairs, but lack anthocyanin.

Other buds are somewhat similar, differing only in size, shape, and

Fig. 4,15.

Buds, bud scales, leaf primordia, and developing leaves.

1. terminal bud of spur shoot
2. terminal bud of basal shoot
3. axillary bud of basal shoot
 - a. outer scales
 - b. inner scales
 - c. leaf primordia
 - d. appearance of c after the bud has opened

(diagrammatic, not to scale).

1.



a



b

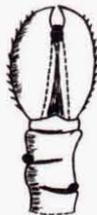


c



d

2.



a



b



c



d

3.



a



b



c



d

number of individual organs (figure 4,15). Overwintering buds of seedlings are equally specialised, though much smaller. On the other hand, at the apex of subterranean stems, only two or three fleshy scales enclose several foliage leaf primordia, the oldest of which have distinct lamina portions.

Bursting of buds follows a similar course each year, though there are differences in time of bud break according to temperatures experienced. The sequence for 1962 at Dry Creek, the coldest field site, is described. Second-year and older seedlings were the first plants to unfold new leaves. Bud movement on some of these plants began on 4 August, and three weeks later most of them had unfolded two or three leaves. By this time buds in the canopy of mature plants were visibly swollen, and by 20 September the inflorescence buds were at the "green finger" stage. These latter had unfolded several leaves by 4 October, and by 9 November all plants were in full leaf, flower buds could be felt between the subtending scale leaves of the most advanced shoots, and new basal shoots began to appear. Plants had reached this stage on 18 October at Cora Lynn, the warmest field site, and by the end of September in the unheated greenhouse at Lincoln.

Apical buds usually burst before axillary buds, though in vigorous, one-year-old shoots the latter often open first. Buds which do not develop inflorescences or vegetative shoots in the spring following their formation remain dormant (latent) unless activated by the death, injury, or senescence of shoots above them.

When typical apical buds open the two outer scales remain unchanged, the petiolar portions of inner scales increase in size

though the lamina remain atrophied, and leaf primordia become normal foliage leaves. Buds formed in exposed habitats may produce 10 or 12 scales before the first foliage leaf appears, whereas with those formed in deep shade, the fifth or sixth scale becomes the first foliage leaf (figure 4,16).

Leaves present as primordia in winter inflorescence buds unfold, the internodes elongate, and the apex produces one or more flowers. In winter vegetative buds the leaves present as primordia unfold with little internode elongation and a "pseudobud" of leaf stipules is formed. Plants complete these processes usually by mid-January in the Waimakariri catchment.

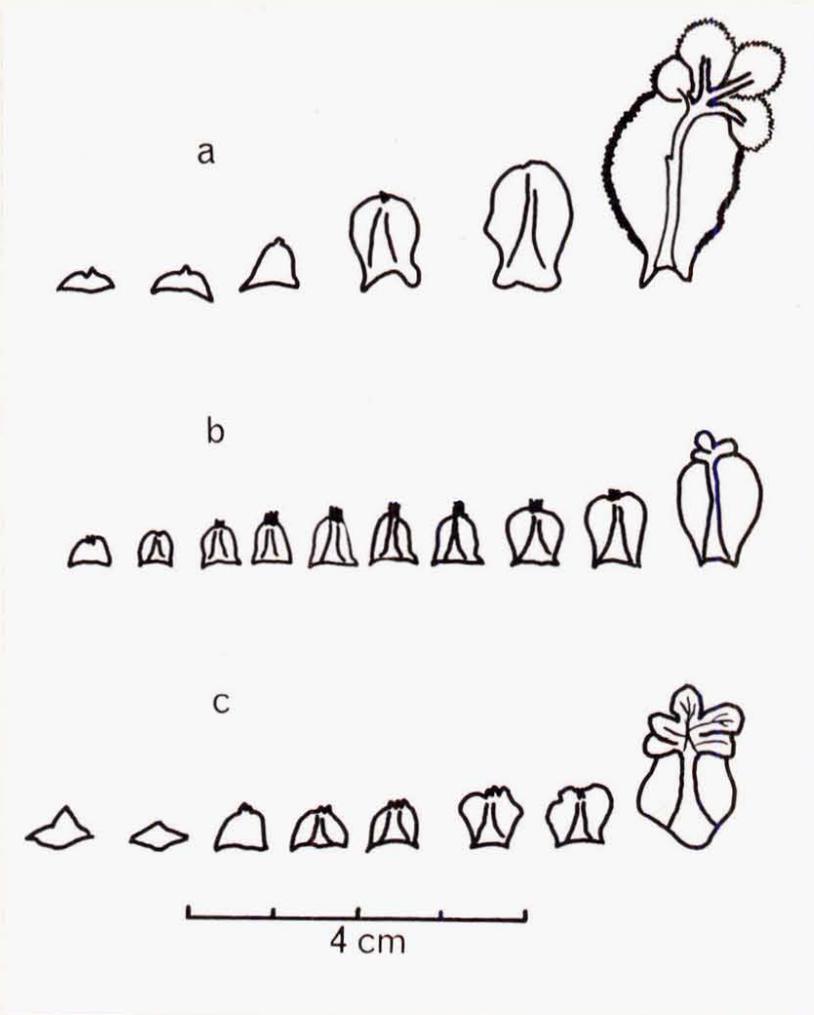
New basal shoots, subterranean stem suckers, and vigorous seedlings unfold more leaves than were present in winter buds and continue growth into late autumn. Buds of such vigorous shoots consist entirely of foliage leaf primordia and are green and succulent.

Winter buds for the next season appear in the axils of unfolding leaves and continue growth and differentiation throughout the summer. By late summer, most of them attain their final size and structure and all the bud scales and leaf primordia are present.

Fig. 4,16.

Appearance of bud scales and leaf primordia after the bud has opened.

- a. terminal bud of basal shoot from the forest habitat at Flock Hill.
- b. terminal bud of spur shoot from the alluvial habitat at Cora Lynn.
- c. axillary bud of basal shoot from the alluvial habitat at Cora Lynn.



432. Experiments

Some knowledge of the seasonal activity of latent buds is desirable for the control of sweet brier by cutting or burning and then spraying subsequent regrowth with herbicides.

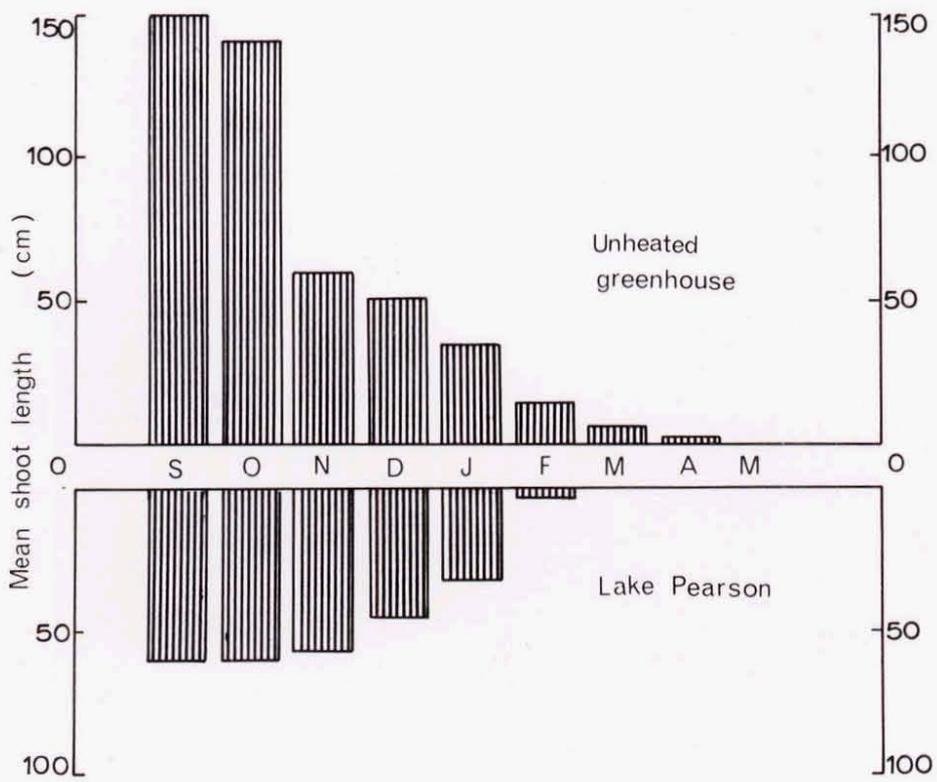
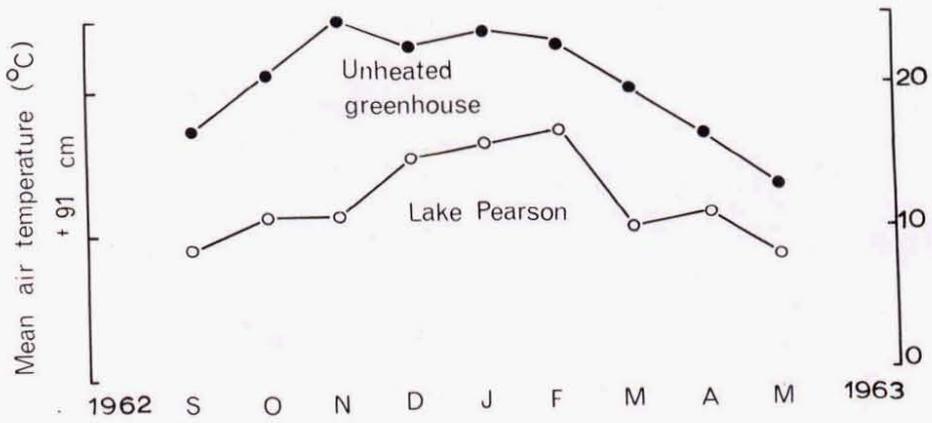
Preliminary experiments in 1961-62 showed that the state of dormancy of latent buds changes during the growing season. Decapitation of shoots early in the season resulted in vigorous outgrowth of basal buds, but if the shoots were cut back later in the season, the same buds remained dormant.

To determine more accurately the time of regrowth and the onset of winter dormancy, plants were successively hard-pruned almost to crown level throughout the 1962-63 growing season. Four-year-old plants growing in the unheated greenhouse at Lincoln, and older plants in a uniform habitat at Lake Pearson, were treated. At the beginning of each month from September onwards, four plants were selected at each site and treated accordingly. When bud activity had ceased in the following autumn, the total regrowth on treated plants was measured and the mean total shoot length calculated for each treatment (figure 4,17).

Decapitation of shoots early in the season resulted in increased bud activity and vigorous regrowth at both sites. Prolonged activity occurred under warmer conditions in the greenhouse. No regrowth occurred after 1 March at Lake Pearson, when buds appeared to be completely dormant. At Lincoln, however, pruning in March and April was attended by some regrowth, and even in May, though regrowth was not visible, the buds of all treated plants swelled and a small amount of sap exuded from the cut shoot stumps.

Fig. 4,17.

Growth of latent basal buds in relation to time
of pruning and mean air temperature, in 1962-63.



It is generally held that shortening days and declining temperatures induce winter dormancy in woody plants; the above results seem to support this belief. The question then arises whether winter dormant buds will resume growth by exposure to high temperatures and/or increased daylength, or whether a period of winter chilling is a prerequisite.

Initial studies 1962:

Newly-germinated seedlings were collected from the field, transplanted in potting soil in porous clay pots, and placed in the unheated greenhouse at Lincoln. When active growth began, one batch was transferred outside to an uncovered cold frame and regular observations were made. This study showed quite clearly that, under warmer greenhouse conditions and natural daylength, buds enter winter dormancy later (4-6 weeks) and leave it earlier (6-8 weeks) than those exposed to natural temperatures and daylength outside.

In another study, four new basal shoots were collected from Lake Pearson at fortnightly intervals after extension growth had ceased. These were cut into segments, each of ten nodes, and stood in water in glass jars. One batch from each collection was placed in a dark room maintained at $22^{\circ}\text{C} \pm 3$, and the other in an unlit refrigerator kept at $5^{\circ}\text{C} \pm 2$. The dark room buds expanded and began to send forth shoots within 3-4 weeks regardless of the time of collection, but the refrigerated buds remained dormant as expected. If the latter were transferred to the dark room, however, buds began growing within 3-4 weeks. It may be noted in passing that the hatching out of aphid eggs (Pentatrachopus tetrarhodus), deposited on these shoots in the field, was similarly affected.

1962/63 studies:

Newly-germinated seedlings raised at Lincoln were potted as above. One batch was placed in the unheated greenhouse, one in the cold frame, and another in a lath house. Again the buds in the greenhouse entered winter dormancy later and left it earlier than those in the cold frame and lath house. Between the latter situations there was no apparent difference in seasonal behaviour.

From the beginning of March 1963, when seedlings in the cold frame showed a decline in activity, three plants at a time were transferred at fortnightly intervals to the following situations:

(1) A growth room kept at $20^{\circ}\text{C} \pm 2$ and artificially illuminated by an overhead battery of fluorescent tubes which ran for 18 hours each day, and a small number of incandescent lamps attached to the side walls, which ran continuously. This gave an average light intensity in the centre of the room of c. 2,000 f.c. for 18 hours, and c. 100 f.c. for the remaining 6 hours each day.

(2) A heated greenhouse in which the night temperature did not fall below 5°C , and subject to natural daylength conditions.

(3) A specially constructed dark cabinet kept at $18^{\circ}\text{C} \pm 2$.

Buds expanded prematurely at all stages of transfer to the growth room from the onset of winter dormancy to natural bud break in the following spring (figure 4,18). Visible outgrowth occurred within two weeks after transfer, even in the most dormant-looking seedlings. In the dark cabinet, premature expansion of buds occurred within four weeks after transfer, but in the heated greenhouse the buds remained dormant until the following spring.

Fig. 4,18.

Examples of premature bud expansion under artificial conditions. The appearance of first-year seedlings 6 weeks after transfer (2/6/63) from the cold frame to the growth room (left) and dark cabinet (right).



New basal shoots were collected from Lake Pearson as in the previous year. One batch from each collection was placed in the growth room; another in the dark cabinet. Buds expanded prematurely in both treatments regardless of the time of collection, though they took longer (4-5 weeks) to move in the dark cabinet. In all the shoot segments used in this study the uppermost axillary (now the terminal) bud expanded first. Buds of basal segments from each shoot proved to be the least active, probably due to their immaturity. Bud activity seemed to be speeded up in "forced" situations by removing the leaves of leafy segments, and the outer bud scales of leafless segments (cf. Wareing, 1956; Nasr and Wareing, 1961).

433. Discussion

Buds of sweet brier can be classified according to their position, function, and state of dormancy.

The basic features of overwintering buds are the red pigment of outer scales, the hairs and glands of inner scales, the somewhat dry outer bud tissues, and dormancy.

In the spring, the vegetative buds of seedlings open first, then the inflorescence buds of mature shoots and finally, basal and subterranean buds of mature plants. This sequence appears to depend on the age of the plant and internal gradients within plants, and is independent of the external environment. However, it can be speeded up or delayed by external factors, particularly temperature.

Newly-formed axillary buds of vegetative basal shoots remain

dormant as long as the apical bud is present and actively growing. If the shoot is decapitated, however, axillary buds begin to grow, with the uppermost suppressing the growth of those below it, consistent with normal apical dominance. In seedlings and juvenile shoot systems, perhaps because of their immaturity, apical dominance is less closely observed, and in the presence of leaves axillary buds of vigorous seedlings usually begin growth in the season they are formed. On the other hand, the fact that suppressed seedlings remain monaxial suggests that external factors such as mineral nutrition, light, and soil moisture are also important.

The experiments indicate that resting buds have no chilling requirement, and that temperature may be the primary factor controlling both the onset of bud dormancy in the autumn and bud break in the following spring. Several points concerning the duration of bud activity were raised (432), but this aspect is treated in greater detail in Section 5 (451).

Under all experimental conditions the pattern of bud development remained constant, and in no case did buds arise from adventitious meristems on shoot segments. Further, when first-year seedlings were decapitated below the level of cotyledons, they failed to give rise to adventitious buds on the epidermis of the remaining hypocotyl. The origin of some crown buds is more obscure; some may be adventitious (421), others may be latent axillary buds whose original position relative to former nodes is difficult to determine.

SECTION 4. AUTUMN LEAF FALL441. Field observations

Leaf abscission is a regular annual process in sweet brier plants growing under natural conditions. For two sites at Flock Hill, the broad relationship in 1962 between leaf-fall and air temperature is shown in Figure 4,19. At both sites leaf-fall began before air temperatures dropped low enough to cause frost damage. The differences in time and duration of leaf-fall between these sites was almost certainly due to contrasting soil moisture conditions (for a full discussion of these sites, see Chapter VI). On the shaded, dark brier site most leaves are green when shed in late autumn, and through the winter plants are rarely completely leafless. On the exposed, sunny brier site prolonged summer drought brings about premature leaf-fall, and before abscission the leaves turn yellow.

Onset and rate of leaf-fall are also genetically controlled. A-type brier plants, for example, are tardily deciduous. Thus in May and June when N type plants have dropped their leaves, A type plants are quite leafy and conspicuous, retaining some leaves throughout the winter and shedding them in the following spring when new leaves are unfolded.

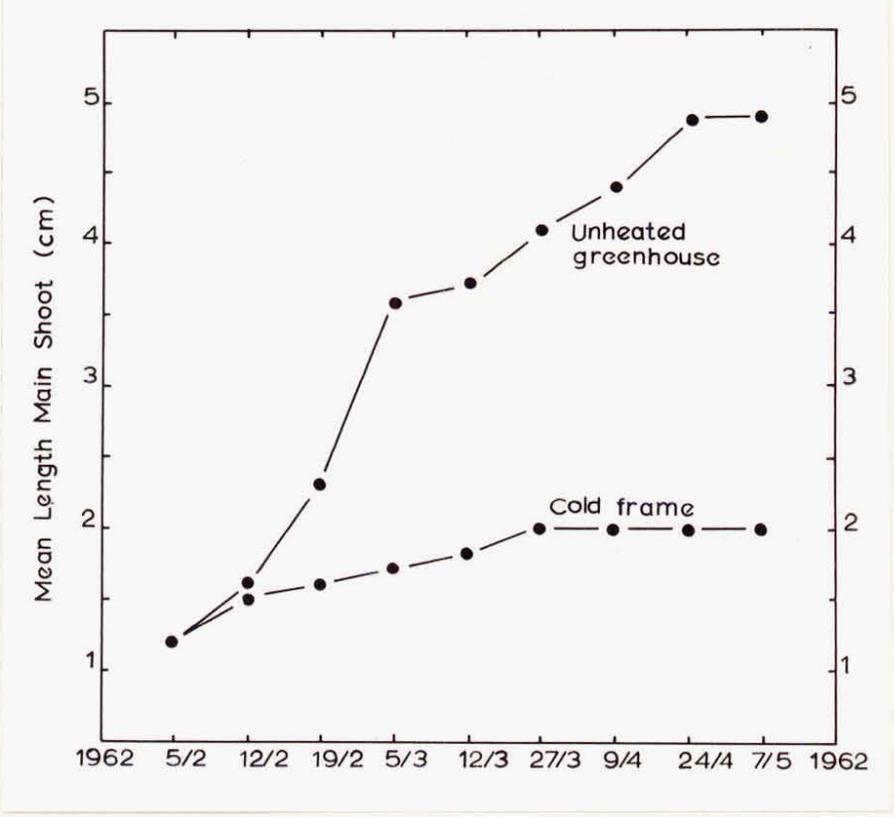
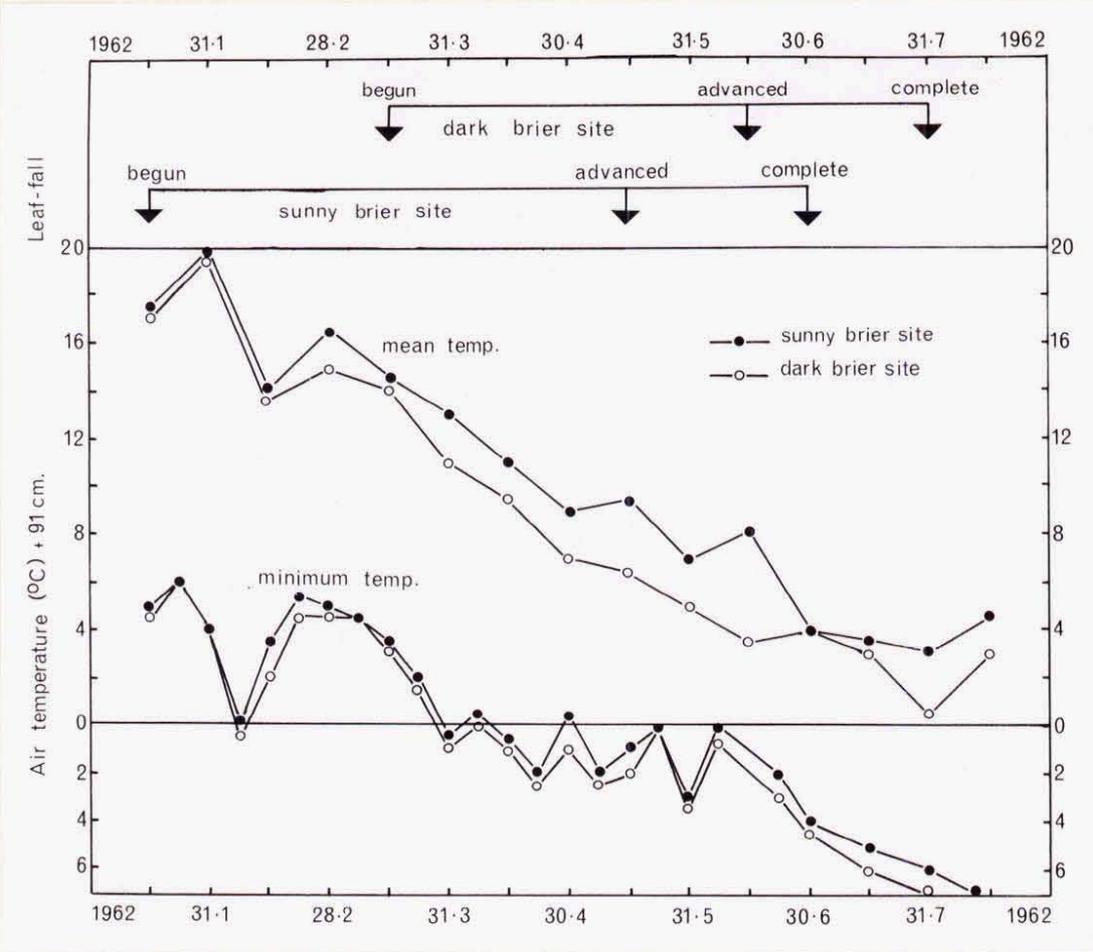
Although some leaves are blown down by wind throughout the summer, most are shed during April and May. As a rule the older leaves are shed first, with vegetative shoot tips and seedlings the last to lose their leaves.

Fig. 4,19.

Leaf-fall on two sites at Flock Hill during 1962,
compared with air temperature.

Fig. 4,20.

Extension growth in transplanted first-year
seedlings.



442. Experiments

First-year seedlings were raised outside at Lincoln in 1962/63 in connection with studies of bud dormancy. On 10 April 1963, six seedlings were transferred to the unheated greenhouse, six to a heated greenhouse, and the remainder were left in the cold frame. No supplementary illumination was provided. Night temperatures occasionally dropped to freezing point in the unheated greenhouse, but did not fall below 5°C in the heated greenhouse which also experienced higher day temperatures.

By the end of May 1963, plants remaining outside had lost all their leaves, whereas in the unheated greenhouse some leaves persisted on most plants until the middle of July. In the heated greenhouse, plants retained their leaves all through the winter.

In November 1962, first-year seedlings raised outside and in the unheated greenhouse were subjected to temperatures of -3°C and -8°C for 17 hours. The former had no ill effects on either material, but the latter proved lethal to both.

443. Discussion

The onset, duration, and completeness of leaf-fall varies within and between sweet brier populations due to internal factors such as age and genetic constitution, and external factors such as mineral nutrition and soil moisture.

Field observations confirm that leaf-fall begins before frost damage occurs, and premature leaf-fall is a feature of all sites subject to soil moisture stresses in summer and autumn. On drought free sites, e.g. the shaded site at Flock Hill, there seems to be a close relationship between leaf-fall and declining mean temperatures.

Experiments showed that leaves of seedlings can withstand temperatures below freezing point; also that leaf abscission can be delayed, even under natural short days, when plants are kept under warm conditions. Thus, if a photoperiodic reaction is present, it is clearly not controlling. It appears that continued sub-optimum temperatures in autumn, without falling to freezing point, may be more important in determining the onset of leaf-fall than reduced daylength.

Similar results have been obtained by other workers for certain species (Wareing, 1956).

The considerable literature on organ abscission reviewed by Addicott and Lynch (1955) and Jacobs (1962) points to natural auxin as the main endogenous regulator in the normal control of leaf abscission. Presumably any factor, internal or external, which causes a decline in the supply of natural auxin or a disturbance of auxin metabolism, leads to leaf abscission.

451. Extension growth

Flowering shoots and short, vegetative laterals have a brief period of extension growth which is usually completed by mid-summer. The duration of this growth is largely predetermined by the number of initials already laid down in resting buds.

Vigorous lateral branches, basal shoots, and subterranean stem suckers begin to grow just before fruiting shoots commence to flower (421). The duration of their growth, together with that of seedlings and juvenile plants, is not predetermined by the number of initials laid down in resting buds, but is controlled by other factors of internal and external origin. Growth of seedlings and basal shoots was observed to study the following points:

- (1) The duration and normal time of cessation of extension growth.
- (2) Factors influencing the cessation of extension growth.

Duration and normal cessation of extension growth:

First-year seedlings from Lake Pearson were transplanted in potting soil in porous clay pots and placed in the unheated greenhouse at Lincoln on 1 February 1962. Prior to this they were still active but slow growing. On 5 February, twelve seedlings were transferred outside to the cold frame and extension growth in both treatments was measured regularly until it had stopped. Figure 4,20 shows that extension growth had ceased by 27 March in the cold frame, and by 24 April in the unheated greenhouse. The warmer conditions of the greenhouse prolonged extension growth and increased the rate and total growth of the main stem.

In another study, 24 3-year-old plants were established in the unheated greenhouse, a cold frame, and in the West Block at Lincoln in spring 1961. In July 1962, all plants, together with eight older plants at Lake Pearson, were hard-pruned almost to crown level to promote the growth of new basal shoots. After growth had begun, all except one of the new basal shoots were pruned off and extension growth was measured regularly until it had stopped (the cold frame study was discontinued after 26 November because the plants were shifted. The Lake Pearson study was also abandoned because of excessive grazing damage to young growth).

Figure 4,21 shows that extension growth had ceased by 19 February in the West Block, and by 11 March in the unheated greenhouse. At Lake Pearson the indications were that extension growth in undisturbed plants had also ceased by mid-February. Thus, basal shoots cease growing several weeks before the parent plants become winter dormant (cf. figures 4,17 and 4,21).

Vigorous seedlings appear to have a longer period of extension growth than lateral branches, basal shoots, and subterranean stem suckers of disturbed or undisturbed plants, perhaps because of their immaturity.

Effect of temperature and daylength:

(1) Initial studies

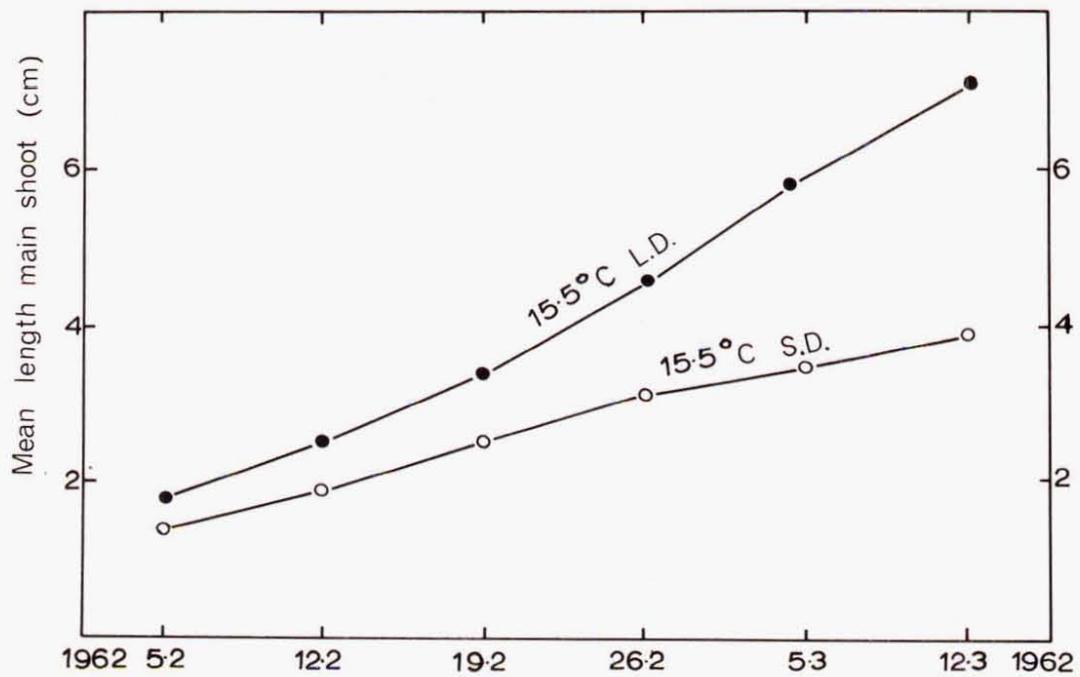
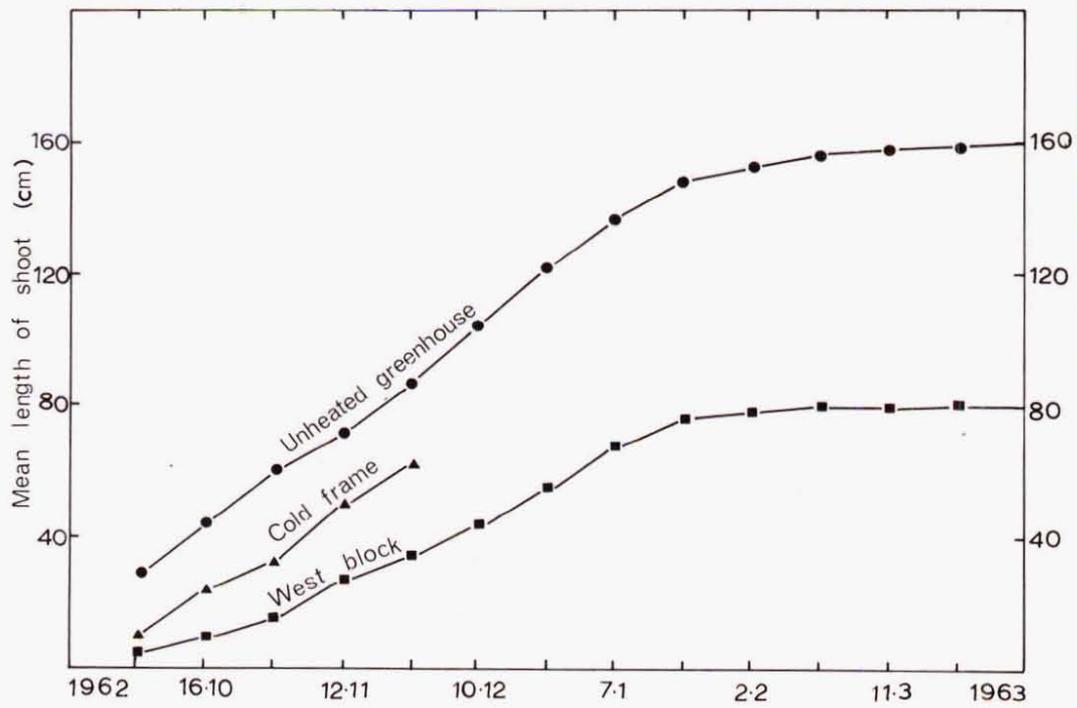
First-year seedlings were subjected to different temperatures and photoperiods in controlled climate cabinets. The light source came from batteries of fluorescent tubes and a small number of incandescent lamps amounting to c. 10% of the total wattage. Light

Fig. 4,21.

Extension growth in promoted basal shoots of
4-year-old plants.

Fig. 4,22.

Extension growth in first-year seedlings in
relation to temperature and daylength.



intensity was maintained at c. 3,500 f.c. at plant height in the centre of each cabinet.

An initial study was begun in March 1962. Wild first-year seedlings were collected in January, transplanted in 4 in. clay pots, and placed in the unheated greenhouse until active extension growth had recommenced. Two groups, each of 12 plants, were then selected by eye and exposed to the following conditions (the remaining transplants were moved to the cold frame outside):

- (1) 15.5°C (60°F) and short days (S.D.) of 8-hour photoperiods.
- (2) 15.5°C (60°F) and long days (L.D.) of 16-hour photoperiods.

Measurements of the main shoot length were made before the treatments began on 5 February and were continued weekly until 12 March, after which date the treatments were discontinued.

Marked elongation of the main axis occurred under long days, but under short days there was a reduction in total growth attributable to reduced internode extension (figure 4,22). On 13 March all the S.D. plants and six L.D. plants were transferred to the unheated greenhouse. The remaining L.D. plants were exposed to higher temperatures ($20^{\circ}\text{C} \pm 2$) and continuous light in a growth room at Lincoln. Measurements of shoot length were continued at each station until 21 May.

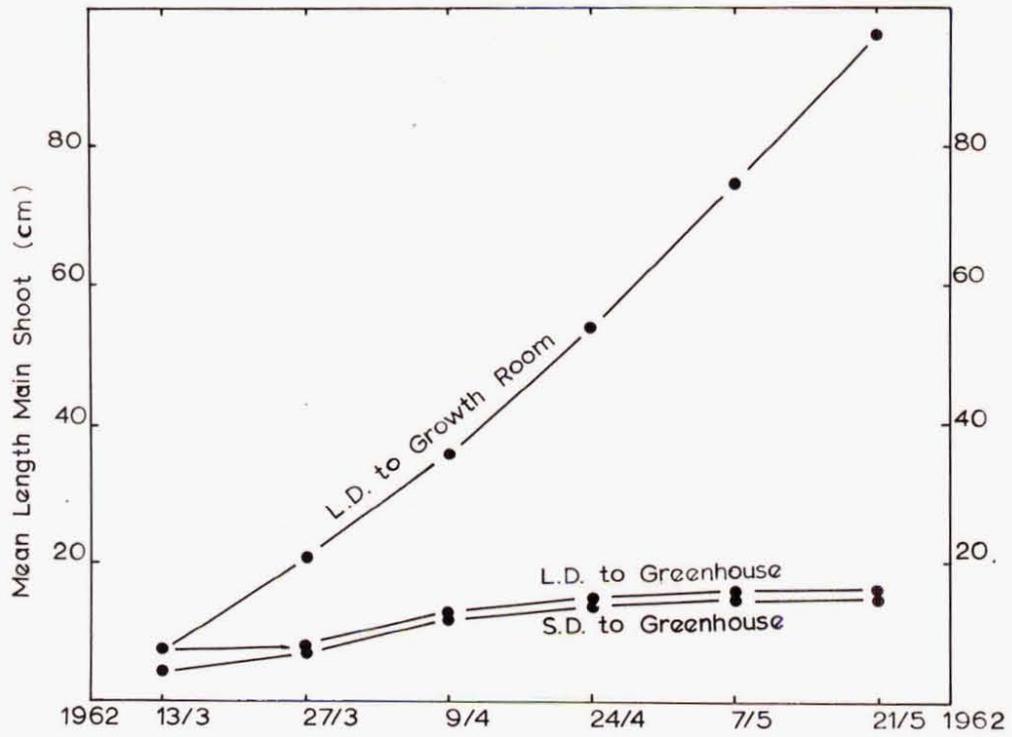
Plants moved to the greenhouse ceased extension growth by the end of April, thus confirming earlier observations, but those in the growth room maintained active growth (figure 4,23). After six months' treatment these plants were still actively growing (figure 4,24).

Fig. 4,23.

Extension growth in first-year seedlings after transfer from the controlled climate cabinet.

Fig. 4,24.

Effects of continuous light and high temperature (right), and natural daylength and temperature out of doors (left). Both plants are the same age - 12 months.



(b) 1962/63 studies

Newly-germinated seedlings were grown in 5 in. porous pots and placed in the unheated greenhouse to encourage active extension growth. On 15 November five groups, each of 12 plants, were selected by eye and exposed to the following conditions:

- (1) 15.5°C (60°F) and 8-hour photoperiods (S.D.).
- (2) " " 16-hour " (L.D.).
- (3) 9°C (48°F) " 8-hour " (S.D.).
- (4) " " 16-hour " (L.D.).
- (5) natural temperature and daylength in the unheated greenhouse.

Measurements of the main shoot length were made before the treatments began and were continued until 11 January 1963, after which date the treatments were discontinued. All treatments were watered with a complete-nutrient solution every fortnight. However, this did not prevent a temporary growth suppression in the greenhouse where plants tended to become "pot-bound" because of rapid growth.

Figures 4,25 and 4,26 show the interaction between temperature and daylength. At 15.5°C plants continued to grow under long days but slowed down under short days, thus confirming earlier results (cf. figure 4,22). At 9°C growth was greatly reduced and long days had only a slight effect. This type of interaction is well known in woody plants. Generally the effect of the dark period is to reduce growth, especially at high temperatures. Low temperature (9°C) resulted in reduced extension growth, attributable to a smaller number of internodes and less internode extension. The reduction in height under short days was attributable mainly to reduced internode extension (table 4,20).

Fig. 4,25.

Extension growth in first-year seedlings in relation to temperature and daylength.

Fig. 4,26.

Examples of first-year seedlings subjected to different temperatures and daylength.

Treatments left to right:

greenhouse
15.5°C L.D.
" S.D.
9°C L.D.
" S.D.

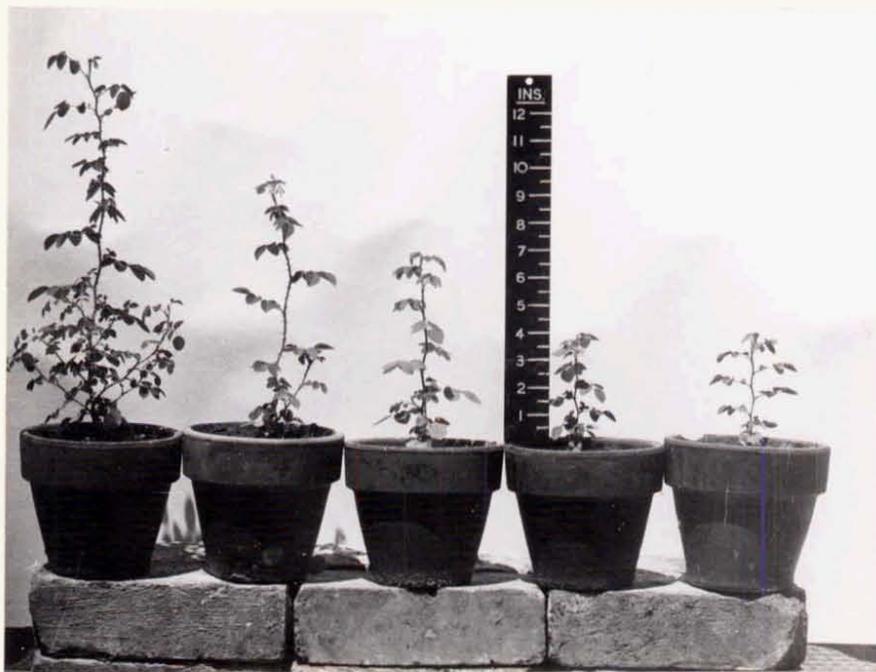
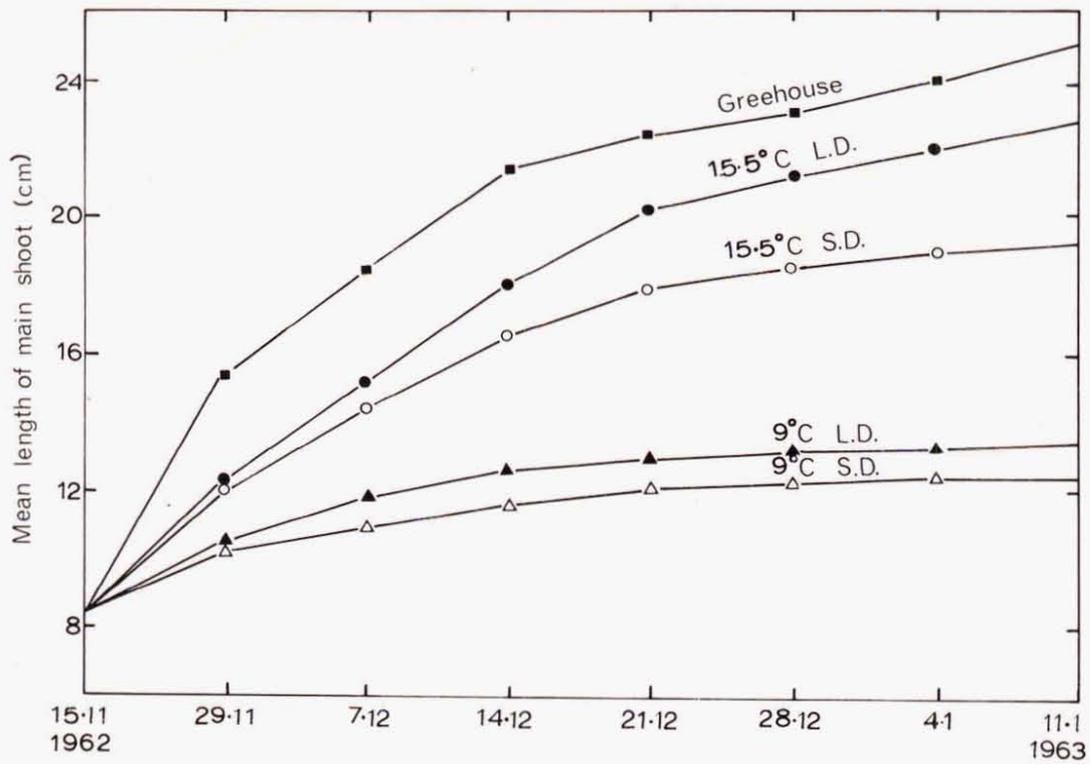


Table 4,20. Effect of temperature and daylength on sweet brier seedlings.

<u>Treatment</u>	<u>Mean shoot length (cm)</u>	<u>Mean No. internodes</u>	<u>Mean internode length (cm)</u>
15.5°C L.D.	22.9 (14.7)	15.6 (6.5)	1.5 (2.3)
S.D.	19.1 (10.7)	15.7 (6.2)	1.2 (1.7)
9°C L.D.	13.6 (5.3)	13.6 (4.5)	1.0 (1.2)
S.D.	12.5 (4.3)	13.5 (4.2)	0.9 (1.0)

(figures in brackets represent mean growth increments during the experiment).

Maximum growth occurred in the greenhouse where plants were exposed to higher temperatures, higher humidities, and natural photoperiods (c. 12 hours) of higher light intensity and probably different light quality compared with conditions in the growth cabinets. This indicates that factors other than temperature and the length of the photoperiod are involved.

452. Cambial activity

A transverse section through an internode of a mature shoot of sweet brier shows the pith, wood, and bark arranged in concentric zones, and prominent vascular rays.

Increase in diameter is due to the production of secondary tissue by the vascular cambium. Each growing season the cambium of sweet brier produces a new increment of wood (secondary xylem) several cells thick and arranged in concentric rings visible to the naked eye. The fact that these rings are annual was confirmed with seedlings and young shoots whose age could be verified from bud scale scars.

The wood of sweet brier is distinctly ring-porous, and is divided into two parts: the early wood, consisting of large vessels up to 0.09 mm in diameter, and late wood of thick-walled tracheids and wood fibres.

An attempt was made to follow the cambium and its xylem derivatives through a seasonal cycle in seedlings, mature canes, and new basal shoots. Transverse sections were taken by hand, stained with safranin and fast green, and mounted in Canada balsam. When the cambium is dormant, cambial cells abut directly upon fully lignified tracheids of the wood which take up the safranin. When the cambium is active, there is a transitional zone about 2-3 cells wide between the cambial cells and the wood of partly lignified elements, which takes up the fast green.

Seedlings:

Second-year seedlings raised in the unheated green-house showed no sign of cambial activity on 15 July 1962, though the apical buds were visibly swelling. The first new vessels were present on 8 August when buds were at the "green finger" stage. On 24 August, when most seedlings had unfolded 2 or 3 leaves, a complete ring of vessels two cells wide was present. Sections showed that secondary growth had resumed rapidly throughout the main axis just before the buds actually opened, thus conforming to the characteristic pattern of cambial initiation in ring-porous species.

Vessel formation in the spring is followed by the formation of summer tracheids. After a period of rapid summer growth there is a gradual slowing down in the formation of new cells. In the greenhouse,

cambial activity ceases shortly after extension growth stops in mid-April, and the transitional zone of partly lignified elements is reduced to zero. By this time the increment of new growth is many cells thick and up to 2 mm wide. In suppressed wild seedlings, on the other hand, growth in diameter is very slow and is often restricted to a narrow ring of small vessels and a band of summer tracheids 2-3 cells wide.

Mature canes:

The pattern of cambial initiation in mature canes is similar to that of seedlings. The first new vessels are present throughout the branches and main axis just before the inflorescence buds finally open. The period of most rapid growth of the xylem occurs in spring and early summer, after which time it gradually slows down. Sections showed that cambial activity was virtually completed by mid-January.

The width of different annual rings in the same shoot varies with environment and also the age of the shoot; the first two or three rings are usually much wider than subsequent ones. Suppressed shoots show a similar restriction of xylem growth to that of suppressed seedlings.

New basal shoots:

In vigorously growing basal shoots which emerge in early summer, differentiation of primary vascular tissue is succeeded gradually by the formation of secondary vascular tissue as the growing point is carried upward by rapid elongation of the proximal internodes. Growth of secondary xylem is most rapid in summer, gradually slowing down in autumn. As with other shoots, new cell production by the cambium

ceases shortly after extension growth stops. Table 4,21 gives the dimensions of various tissues, except the primary vascular tissue, at the end of the growing season.

Table 4,21. Radial dimensions of various tissues in a typical basal shoot after the first season's growth.

Distance from apex cm -----	Total width of shoot mm -----	Width of pith mm -----	Width of wood mm -----	Width of bark mm -----
2	2.0	0.9	-	0.4
20	3.0	1.8	0.1	0.4
50	5.8	4.0	0.4	0.4
100	10.7	7.7	0.8	0.6
200	16.6	9.2	2.7	0.9
300	16.8	7.0	4.0	0.8

At the base of these shoots after the first season's growth pith, primary vascular tissue, wood, and bark occur as concentric zones. The wood becomes progressively narrower towards the shoot apex, finally petering out below the apical bud, behind which small groups of primary vascular tissue surround the pith. This indicates that as length growth of the internodes ceases, growth in diameter takes place.

Three important points emerge from these observations:

- (1) Cambial activity in mature shoots begins before the aerial buds finally open.
- (2) It begins almost simultaneously throughout the shoot.
- (3) Its maintenance seems to depend upon active extension growth.

1962/63 studies:

It is generally accepted that initiation and control of cambial activity depends upon the production of free auxin by expanding buds,

moving in a basipetal direction and spreading more quickly in ring-porous species. When extension growth stops, auxin production falls and cambial divisions cease.

To determine whether renewal of cambial activity in sweet brier is dependent on the presence of expanding buds, new lateral branches of mature plants were treated in the late autumn of 1962 as follows:

- (1) One branch was completely debudded.
- (2) Another was partly debudded, i.e., only the axillary buds were removed.
- (3) A third branch was left intact.

By mid-January 1963, the intact branch had produced flowering shoots which bore fully-formed hips. The apical bud of the partly debudded branch had also expanded into a flowering shoot bearing fully-formed hips. The completely debudded branch remained dormant and no adventitious buds arose. Sections were taken through each branch to determine the extent of new xylem for the 1962/63 growing season.

Table 4,22. Width of new xylem (mm) in intact, partly debudded, and completely debudded lateral branches for the 1962/63 growing season.

<u>Distance from apex (cm)</u>	<u>Intact branch</u>	<u>Partly debudded</u>	<u>Completely debudded</u>
4	0.36	0.25	+
10	0.54	0.072	+
50	0.74	0.036	+
100	1.26	+	+

+ no new xylem formed.

This study supports the view that renewal of cambial activity in the spring is dependent on the presence of expanding buds. In the partly debudded branch, new vessel production petered out as the distance from the active apical bud increased. In the fully debudded branch the cambial zone was brown in colour and the cells appeared dead. However, there were one or two new vessels between the xylem rays throughout this branch. Since no adventitious buds were stimulated by debudding, and since it is unlikely that the date of debudding post-dated dormancy, a probable explanation for their development is that advanced by Wareing (1951) to account for the rapid resumption of secondary growth in ring-porous species, viz., the presence in the cambium of a reserve of auxin-precursor from the previous year.

453. Discussion

The duration of extension growth in sweet brier is subject to a variety of modifying influences of both internal and external origin. It varies with the age of the plant, the type of shoot, and the external environment. It follows a gradient from canopy shoots through replacement shoots to vigorous seedlings which have the longest period of extension growth, perhaps due to their immaturity and favourable supplies of nutrients and soil water.

The interaction between temperature and photoperiod in reducing the period of extension growth was demonstrated for sweet brier seedlings under experimental conditions. Extension growth is maintained continuously if plants are exposed to continuous artificial light of low intensity and high temperatures. It appears that reduced

temperatures may be the primary factor controlling the cessation of extension growth in nature.

The onset of cambial activity in established shoots depends upon the presence of expanding buds, and is clearly climatically controlled. The duration of cambial activity, however, varies with the age and time of emergence of different shoots. It depends upon active extension growth which in turn depends upon internal ageing processes as well as the external environment.

In this study, the presence of new xylem elements (vessels) was used as an indication of cambial activity because of the prevailing concept that xylem and phloem production occur simultaneously. Evert (1963), however, has shown that phloem differentiation precedes xylem differentiation in Pyrus malus (Rosaceae) by about $1\frac{1}{2}$ months, though both cease almost together.

These seasonal growth patterns of sweet brier are of prime importance in its adaptation to the New Zealand tussock grassland environment which is noted for long cold winters and a short yet active growing season. Unlike many other woody plants, the seasonal activity of sweet brier seems to be markedly affected by temperature conditions and is apparently not subject to photoperiodic control. This view derives from the evidence in this study and the fact that roses generally do not need a rest period in winter or at any other time of the year. Given adequate nutrients, water, and high temperatures, plants will grow continuously, even under natural short days.

SECTION 6. THE ROOT SYSTEM461.Seedlings:

The first lateral roots of newly-germinated sweet brier seedlings usually appear before the first foliage leaf unfolds and are somewhat finer than the primary taproot which bears them (figure 4,6). First-year seedlings, grown in the unheated greenhouse and with four leaves unfolded, had a freely-branched taproot system with a total root length of c. 100 cm, and an oven-dry weight of c. 0.03 gm. By the end of the summer, these seedlings had developed robust root systems consisting of coarse (70.5 mm diameter) and fine roots with a total oven-dry weight of about 1.4 - 2 gm (figure 4,7). Such robust root systems contrast strongly with the finely branched and deeply descending taproots of wild, first-year seedlings growing on mature soils under grassland (figure 4,27).

Mature plants:

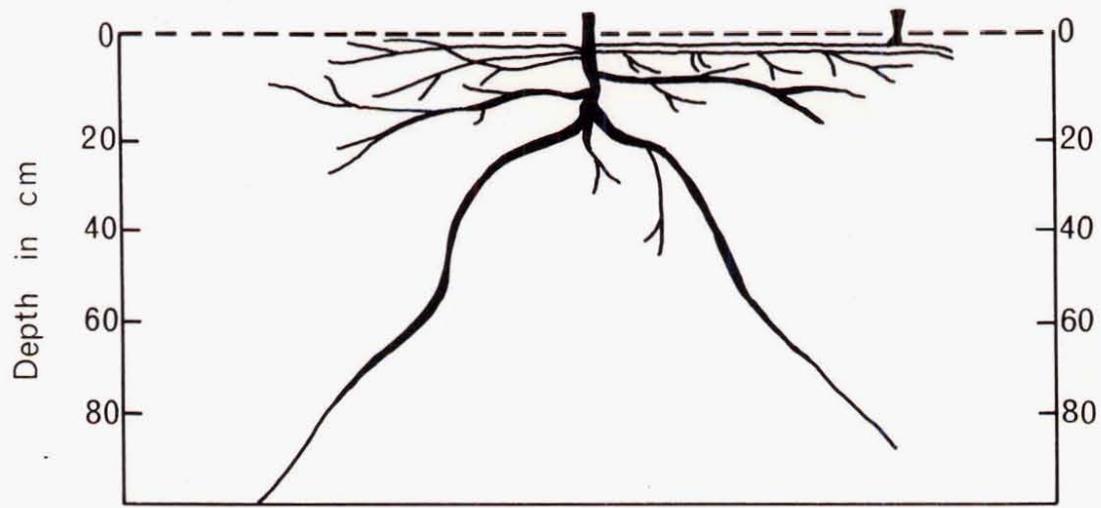
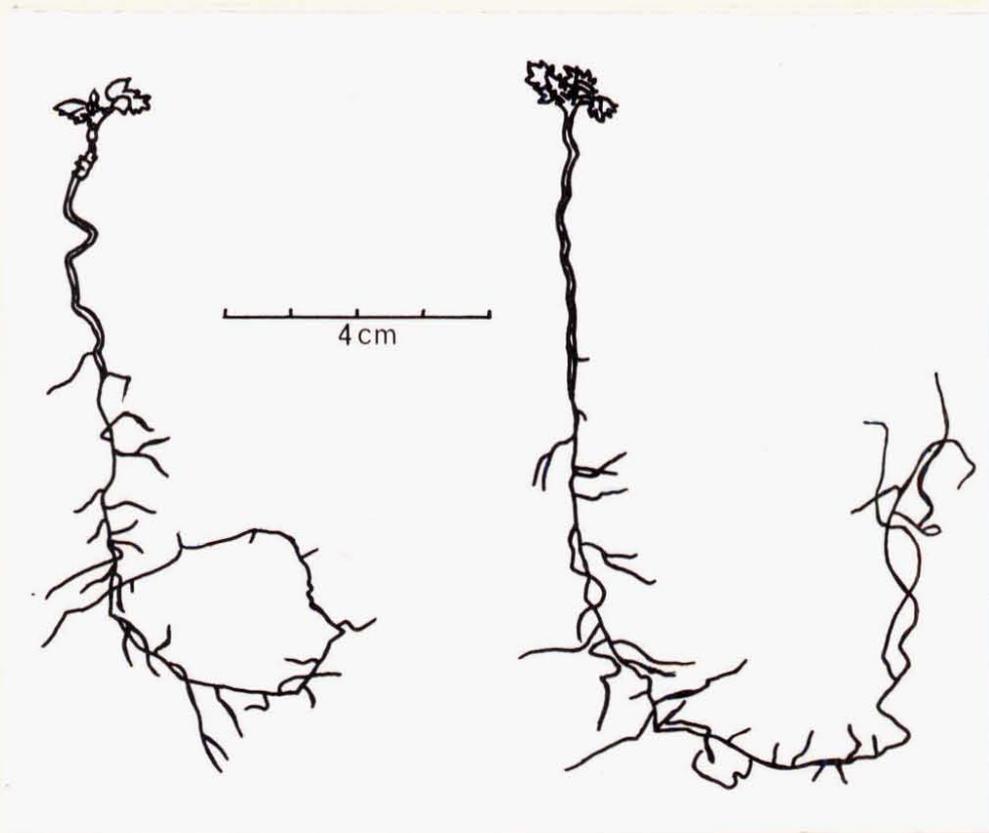
The root system of mature plants is made up of long, radiating, coarse roots up to 4 cm in diameter, finer lateral roots, and freely-branched rootlets (figure 4,28). Most of the coarse major roots radiate out from the proximal region of the original taproot, and at least one or two are deeply descending. The lateral roots are best developed in the proximal region of major roots, while fine rootlets, though fairly well distributed throughout the system, are best developed near the soil surface. Adventitious roots arising from the nodes of old underground shoots are similarly divided, though usually on a much smaller scale. These are also best developed just beneath the soil surface. This system of root distribution is characteristic of most mature plants. However, it is subject to environmental variations, particularly soil conditions (621).

Fig. 4,27.

The root system of wild, first-year seedlings.

Fig. 4,28.

Schematic diagram of the root system of mature plants.



Growth rate and longevity:

Estimates of the growth rate and longevity of major and lateral roots proved to be unreliable because of the indistinct nature of growth rings, especially in the older proximal regions. In cross section the root differs markedly from the shoot. The growth rings are much narrower and less ring-porous. The vessels are larger (up to 0.12 mm diameter), particularly in the younger distal regions, and the cells are less lignified. In addition, the vascular rays are much wider and starch containing to a more marked degree.

The fine rootlets or "feeder" roots rarely exceed 10 cm in length, and are usually branched to more than the first degree. Sections showed that most of them were less than one year old. Examinations during the late winter and early spring revealed that many actually die after one-year's growth. It is clear that most of the feeder roots of sweet brier are short-lived and subject to annual renewal.

Seasonal activity:

The seasonal activity of roots was followed in connection with experiments on extension growth (451). First-year seedlings raised in 4in. pots in the unheated greenhouse were lifted on 24 April 1962 after extension growth had virtually ceased. By this time, several roots had penetrated through the bottom of each pot. All were white in colour and the finer rootlets were well supplied with root hairs. Obviously they were still active. The protruding roots were pruned off level with the bottom of the pot in some cases, while others were left intact after carefully noting the extent of the root system. All pots were then set up in a fresh mixture of coarse aggregate and

fine sand which was kept moist but never allowed to become fully saturated. The pots were lifted again on 10 June and the roots examined. In the pruned treatment, the roots had again grown through the bottom of each pot, attaining lengths of up to 6 cm. The unpruned roots had also extended their original systems. Nearly all roots were light brown in colour and apparently dormant. This clearly demonstrates that roots continue meristematic activity long after shoots cease extension growth.

The same pots were carefully reset back in position. On 20 July they were lifted again and the roots examined. By this time, the apical buds of shoots were visibly swelling but none had actually opened. New roots up to 1.5 cm in length were observed in every case. All were white in colour, and the pale yellowish meristematic region of root tips was plainly visible. This demonstrates that roots commence growth before the aerial buds finally open in the spring - in this there is an analogy with the initiation of cambial activity in shoots.

I have no information on soil temperature limits between which the growth of sweet brier roots can take place. But observations of plants close to a field station of the Department of Agriculture, Broken River, indicate it occurs between temperatures of 5° and 22°C . Practising horticulturalists consider that a soil temperature above 27°C is too high for normal root growth in cultivated roses.

CHAPTER 5

EFFECT OF SOME ENVIRONMENTAL FACTORS ON SEEDLING GROWTH

INTRODUCTION

Sweet brier is subject to a variety of conditions affecting seedling growth because of its wide distribution.

Attempts were made to compare seedlings growing on sites which appeared to differ in one factor, but were otherwise similar. Field work was confined largely to the Waimakariri catchment, North Canterbury. Some environmental factors were measured and are discussed in greater detail in the following chapter. Experiments were designed to resolve certain problems of seedling growth in the field. These were carried out at Lincoln where conditions could be reasonably controlled.

SECTION 1. THE LIGHT CLIMATE511. Field observations

Variations in light intensity in the field are often accompanied by variations in temperature, humidity, light quality, and soil moisture, and in this study the "light climate" is regarded as a complex of factors. The following data are presented on the understanding that only broad ecological inferences can be drawn.

First-year seedlings:

Seedlings collected from Flock Hill in January 1963 were subjected to the following measurements: length and fresh weight of stems including the hypocotyl; number of nodes (leaves); area and fresh weight of the fourth leaf. The latter was chosen because of its uniform shape and number of leaflets, and because the first two or three leaves

had usually abscised. Leaf area was determined by an air-flow planimeter previously described (212).

The sites compared at Flock Hill were: a stand of manuka scrub and sparsely vegetated alluvium, both on the sunny brier site; and under a closed canopy of beech forest on the dark brier site. At each site light readings were taken with a photocell during several summer visits. Readings were taken as quickly as possible around noon on overcast days, and the results were combined to give an approximate expression of light intensity. Table 5,1 shows the results.

Table 5,1. Average dimensions of wild first-year seedlings in relation to light intensity. N = 20 plants.

(a) Mean dimension of organs.

(b) Ratio weight of organ/dimension of organ.

(a)

Site	Light intensity (daylight=1.0)	Stem		4th leaf		No. of nodes
		Length mm	Weight mgm	Area mm ²	Weight mgm	
Alluvium	1.0	43	17.4	24	5.8	7
Scrub	0.4	66	24.2	64	8.2	7
Forest	0.2	41	14.1	101	8.2	4

(b)

Alluvium	1.0	0.40	0.24
Scrub	0.4	0.36	0.13
Forest	0.2	0.34	0.08

Plants in full daylight had smaller leaves than shaded plants, and the largest leaves were formed under deep shade. The length of stems

also increased with shading, but under deep shade there was a reduction in mean stem length attributable to a smaller number of nodes. Although the size of organs generally increased with shading, the ratio weight of organ/dimension of organ decreased, with the leaves being particularly sensitive to varying light intensity.

Older seedlings:

Measurements of older seedlings in the field present some difficulties. In open sites plants are subject to insect attack, animal grazing, and frost damage, while in shaded habitats fungal infection may be severe. The latter is considered an important facet of the light climate of shaded seedlings. Moreover, differential growth rate may result from genetic variability which is difficult to determine in the seedling stage.

A comparison of four-year-old plants shows that the tendency for rapid growth in the first year under shade does not seem to apply in subsequent years.

Table 5,2. Average growth of four-year-old plants in relation to light intensity. N = 20 plants.

Year	1959	1960	1961	1962	Total	Weight
<u>Stem increment</u>	<u>mm</u>	<u>mm</u>	<u>mm</u>	<u>mm</u>	<u>mm</u>	<u>mgm</u>
1.0 daylight	30	32	48	85	195	173.0
0.4 daylight	58	28	22	23	131	83.6

Shaded seedlings may remain monaxial for several years as the following measurements of an eight-year-old plant show

Year	1956	57	58	59	60	61	62	63
Stem increment (mm)	57	27	18	22	8	18	27	25

Such plants usually become decumbent since they form little wood and their stems are weak. The end result is a moribund plant which seldom survives.

Adult plants rarely originate from suppressed shaded seedlings. Some may arise in the better light of the forest edge or in clearings, while shoots may eventually penetrate a canopy of dense scrub or grow up between the gaps.

512. Experiments

The effects of varying light intensity on seedling growth were studied in greater detail at Lincoln using three cold frames. There were three levels of light intensity: full daylight (1.0), and approximately 0.75 and 0.5 daylight by use of light wooden frames covered with steel gauze of different gauge. On 26 September 1962, newly-germinated seedlings raised at Lincoln from the same provenance (Lake Pearson) were planted in 6" porous pots containing equal parts of loam, sand and sterilised compost, but no added nutrients. Seedlings were then placed in the unheated greenhouse until required.

On 22 October, 8 groups each of 8 plants were matched by eye. Two groups were assigned at random to each light treatment; one was harvested immediately; and one was left in the greenhouse and is discussed later in this subsection. All pots were numbered, randomised, and kept widely spaced to avoid mutual shading. Plants were watered regularly, and at weekly intervals re-randomised and sprayed with fungicide to discourage powdery mildew. One group from each treatment

was harvested on 22 November and the other on 22 December. The harvest procedure was as follows: plants were removed from the pots and the roots washed free of soil, then each plant was divided into roots, stems, leaves, and hypocotyl. After the organs were counted and measured, all samples were oven-dried at 100-105°C and weighed. Table 5,3 shows the average yields at each harvest.

Cold frame experiment

Table 5,3. Average dimensions (mgm and cm²) of plants in experiment on light and growth.

Treatment	0.5 daylight		0.75 daylight		1.0 daylight		
	Harvest	22/10	22/11	22/12	22/11	22/12	22/11
No. of surviving plants	8	8	8	8	7	8	7
Weight of roots	28.8	76.2	498.6	152.4	589.8	310.0	1117.3
Weight of hypocotyl	5.5	16.7	74.3	23.6	73.7	32.5	116.7
Weight of leaves	35.8	211.0	780.9	354.0	634.3	547.6	1020.7
Weight of stems	10.7	85.3	499.2	155.5	587.8	247.3	562.0
Total weight	80.8	389.2	1853.0	685.5	1885.6	1137.8	2816.7
Leaf area	8.3	53.5	172.8	74.2	144.9	80.2	112.2

The total plant weight increased from the initial (22/10) to the final harvest in all treatments, with the greatest increase occurring in full daylight. The total leaf area likewise increased, but the highest value was attained in the darkest treatment.

There were some marked qualitative differences. At the final harvest, plants in 0.5 daylight were somewhat decumbent, sparsely branched,

and clad with a few soft prickles. The leaves were thin and dark green, sparsely clad with hairs and glands, and distinctly flattened. The roots were thick, smooth and unbranched, and poorly distributed throughout the pots. On the other hand, plants in full daylight were upright, bushy, and heavily armatured. The leaves were fleshy and yellowish, densely clad with hairs and glands, and distinctly folded. The roots were thin, finely branched and copiously supplied with root hairs, and well distributed throughout the pots. In addition, all aerial organs were deeply stained with anthocyanin. Plants in 0.75 daylight were intermediate in most respects (figure 5,1).

The technique of "growth analysis" was applied to the data from each harvest; first, as a measure of the efficiency and capacity of the photosynthetic system in the different light treatments, and second, to compare the results with the published accounts of Blackman and others on herbaceous plants. Unfortunately, the interval of 4 weeks between harvests was too long (cf. Williams, 1946), and plants in the better lighted treatments suffered from a growth depression during the second interval as they became more and more pot-bound. Thus, the relationship between leaf area and plant weight at successive intervals was non-linear (figure 5,2), and estimates of growth increments over the entire experiment are subject therefore to considerable bias (Williams, 1946). However, if it is assumed that nutrients and water were adequate for active growth in all treatments during the first interval of 4 weeks, then errors of this kind are likely to be small. With this in mind, the results obtained from the first interval only are discussed.

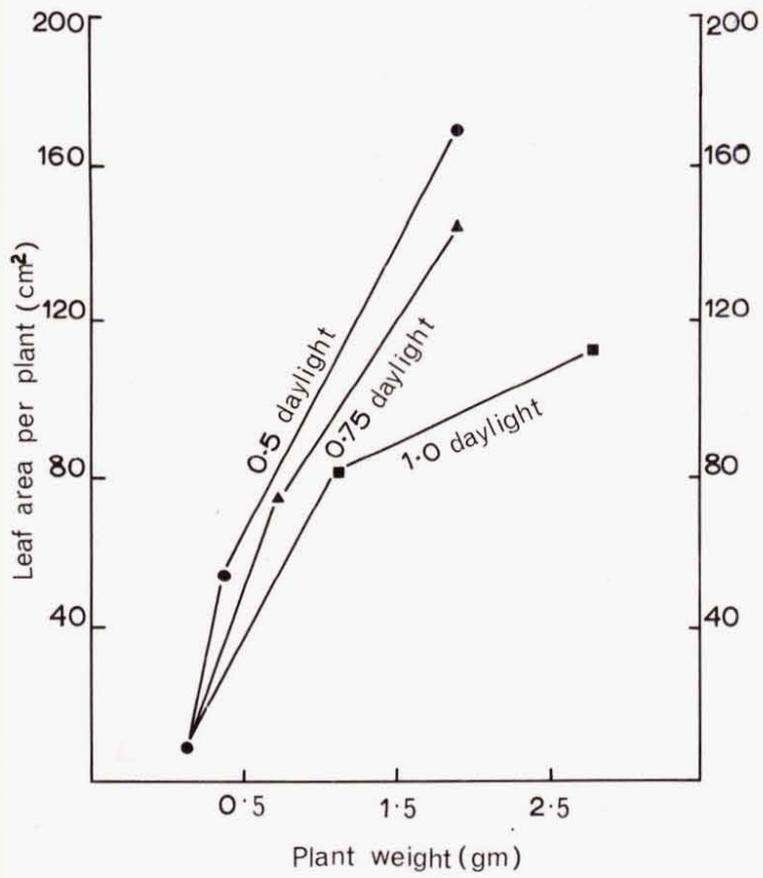
Fig. 5,1.

Representative plants from the experiment on light and growth, at the final harvest.

1. 1.0 daylight
2. 0.75 daylight
3. 0.50 daylight

Fig. 5,2.

Effect of varying light intensity on relative changes in leaf area and plant weight at successive sampling occasions.



The rate of increase of dry matter per unit of leaf area, or net assimilation rate (NAR), is calculated from:

$$\text{NAR} = \frac{W_2 - W_1}{A_2 - A_1} \times \frac{\log_e A_2 - \log_e A_1}{t_2 - t_1}$$

where W_1 and W_2 are the weights of plants, A_1 and A_2 the leaf areas, at times t_1 and t_2 (W_1 and A_1 are the weights and leaf areas respectively of the initial harvest). The following values were calculated for the first interval, 22 Oct. - 22 Nov., from the data of separate plants.

Table 5,4. Net assimilation rates (g/dm²/week).

Treatment	0.5 daylight	0.75 daylight	1.0 daylight
Harvest	22/11	22/11	22/11
Mean NAR	0.28	0.45	0.69
S.D. of mean	0.09	0.11	0.12

The most important trend during this interval is the significant increase in NAR from the darkest to the best-lighted treatment ($P < 0.01$). The high value attained in full daylight lies well within the mean range of 0.41 - 0.72 g/dm²/week postulated by Heath and Gregory (1938) for most temperate or tropical plants.

Another important relationship is the ratio total leaf/total plant weight, or leaf-area ratio (LAR), calculated from:

$$\text{LAR} = \frac{\frac{A_1}{W_1} + \frac{A_2}{W_2}}{2}$$

The following values were calculated for the first interval from

the means of ratios of separate plants.

Table 5,5. Leaf-area ratios (cm²/g).

Treatment	0.5 daylight	0.75 daylight	1.0 daylight
Harvest	22/10	22/11	22/11
Mean LAR	104	121	87
S.D. of mean	12.8	8.3	4.0

The LAR fell sharply in full daylight, while in shaded treatments it rose, with a significant increase in the darkest treatment

($t = 3.4$; $P < 0.01$).

The relative growth rate (RGR), equal to the product of NAR and LAR, was calculated from:

$$RGR = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1}$$

The following values were calculated from the data of separate plants.

Table 5,6. Relative growth rates (g/g/week).

Treatment	0.5 daylight	0.75 daylight	1.0 daylight
Harvest	22/11	22/11	22/11
Mean RGR	0.34	0.48	0.60
S.D. of mean	0.11	0.09	0.07

The RGR, like NAR, rose during this first interval from the darkest to the best-lighted treatment, and this trend is considered to be a fairly reliable measure of the rate at which the weight of the plants in the various treatments was increasing.

Table 5,7 shows the relations between the weights of separate plant organs at the end of the first interval. The calculations were made using the absolute yields shown in Table 5,3.

Table 5,7. Average weights and ratios of separate plant organs.

- (a) Mean weight of organs on 22/11/62 (mgm).
 (b) Means and standard deviations of individual items.
 (c) Ratio weight of organ/total plant weight (%).

(a)

<u>Treatment</u>	<u>Root</u>	<u>Hypocotyl</u>	<u>Leaves</u>	<u>Stem</u>	<u>Total</u>
0.5 daylight	76.2	16.7	211.0	85.3	389.2
0.75 daylight	152.4	23.6	354.0	155.5	685.5
1.0 daylight	310.0	32.5	547.6	247.3	1137.8

(b)

Mean	179.5	24.2	370.8	162.7
S.D. of items	119.2	7.9	168.9	81.2

(c)

0.5 daylight	19.6	4.3	54.2	21.9
0.75 daylight	22.2	3.4	51.6	22.7
1.0 daylight	27.2	2.8	48.1	21.7

The leaves and roots showed the most and the hypocotyl and stem the least response to varying light intensity. This is demonstrated by the relative size of their deviations. Shading positively decreased the ratio root weight/total plant weight, and increased the proportion of hypocotyl and leaves, while the proportion of stem remained fairly constant.

Although LAR decreased from the darkest to the best-lighted treatment, the ratio leaf weight/leaf area increased.

Table 5,8. Ratio leaf weight/leaf area (averages of each treatment).

<u>Date</u>	<u>0.5 daylight</u>	<u>0.75 daylight</u>	<u>1.0 daylight</u>
22/10	4.31	4.31	4.31
22/11	3.94	4.77	6.82

At the final harvest (22/12) the number and total length of stems attained in all treatments were calculated as follows:

Table 5,9. Average number and dimension of stems on 22 December.

Treatment	0.5 daylight		0.75 daylight		1.0 daylight	
	No.	Length	No.	Length	No.	Length
	<u>stems</u>	<u>cm</u>	<u>stems</u>	<u>cm</u>	<u>stems</u>	<u>cm</u>
Mean	4.7	50.6	6.0	58.4	7.0	63.4
S.D. of mean	2.1	8.4	2.1	21.5	1.2	9.9

Although they suffered from a growth depression during the second interval, plants in full daylight had more but shorter stems than shaded plants. They also had almost twice as many leaves (47 ± 8.8).

Greenhouse experiment:

One group of plants was retained in the unheated greenhouse during the first period of the cold frame experiment. This was also harvested on 22 November and the results are compared with those obtained in full daylight in a cold frame.

Table 5,10. Yields and growth rates of plants in the unheated greenhouse and in full daylight on 22 November.

Treatment		1.0 daylight	Greenhouse
Harvest	22/10	22/11	22/11
Av. total weight (mg)	80.8	1137.8	1410.2
Av. leaf area (cm ²)	8.3	80.2	112.3
Mean NAR (g/dm ² /wk.)	+	0.69 ± 0.12	0.73 ± 0.09
Mean LAR (cm ² /g)	104 ± 12.8	87 ± 4.0	91 ± 4.4
Mean RGR (g/g/wk.)	+	0.60 ± 0.07	0.65 ± 0.09

The light intensity at noon in the greenhouse amounted to c.65% of full daylight, and the mean unscreened air temperature for the period was 24.6°C for the greenhouse and 16.6°C for the cold frame. Weekly values for relative humidity at 10 a.m. were much higher (>15%) in the greenhouse. The latter therefore received less light than the open cold frame, but experienced higher temperatures and humidity, especially at night. The difference in growth between the two treatments, though not significant, is probably a "greenhouse effect" attributable to temperature, and possibly other factors.

Although these results are not directly applicable to field problems, they do suggest that factors other than light intensity are involved in comparisons between shaded and well-lighted habitats.

513. Discussion

In wild first-year seedlings the largest leaves and longest stems are formed under shade. This agrees with the experimental results. The greatest weight also was produced under shade, whereas the experiment indicates that the highest yields are obtained in full daylight. Unlike their wild counterparts, however, the seedlings in the cold frame did not suffer from competition, and nutrients and soil water were adequately supplied, at least during the first harvest interval of 4 weeks.

Although the experiment lacked precision, certain provisional conclusions can be drawn. Shading increases LAR but depresses NAR and RGR. It increases the ratio leaf area/leaf weight and depresses the proportion of root. This is in general agreement with the results of Blackman and others on several herbaceous plants.

Further, several characteristics of seedlings can be directly related to changes in light climate. The following are the most important: size, thickness, colour, degree of hairiness and glandulosity, and pigmentation of leaves; degree of attenuation and wood development in stems; structure and extent of roots; and the incidence of fungal infection.

Although sweet brier seedlings will tolerate light shading, it is apparent that they achieve better subsequent growth in full daylight, and do not appear to survive low light intensities of less than 0.5 daylight. It can be concluded, therefore, that the natural environment for sweet brier is in the neighbourhood of full daylight.

SECTION 2. AIR AND WATER RELATIONS

521. Field observations

Sweet brier seedlings are especially abundant in the neighbourhood of parent plants. This is particularly true of first- and second-year seedlings, but older seedlings occur more sporadically and not necessarily with parent plants.

Populations of older seedlings can generally be divided into the following main categories, and these give some indication of the conditions required for successful establishment.

(1) Rejuvenated soil populations. These are usually found on flat or sloping ground where the vegetation has been modified by man, and the soil surface disturbed by wind, water or gravity.

(2) Linear water channel populations. These mark the high water-level of underground water and periodic floods on flat to undulating ground, or represent frequent flushing of water on sloping terrain. The former includes riverbed alluvium and alluvial terraces, the latter all depressions which act as natural gutters in the event of rainfall.

(3) Colluvial populations. These are frequently found on fans and cones of loose or partly stabilised colluvium at the base of commonly steep slopes.

(4) Rock outcrop populations. Seedlings are often concentrated in crevices and ledges which favour an accumulation of soil in an otherwise bare-rock, environment.

(5) Scattered establishment. Sweet brier seedlings, though usually gregarious, may be found in much smaller groups, or as single

individuals, in various situations at some distance from the nearest populations.

These populations owe their existence not only to local concentrations of seeds, but also to suitable habitats for establishment. Although several factors enter into this, especially light intensity, plant competition, and animal grazing, a set of edaphic conditions prevail in which soil moisture, aeration, and fertility are closely linked (313).

The most striking similarity of these habitats is the near-optimum levels of drainage and aeration of the soils. Heavily compacted and poorly or excessively drained soils have the opposite effect. Not only is the growth of seedlings strongly impaired and reduced to something less than half normal, but the new leaves produced do not have the healthy green colour they should have.

522. Experiments

An attempt was made to demonstrate the effects of different levels of soil water and soil compaction on seedling growth. In addition, the growth of seedlings in exposed and sheltered situations was compared. This set of experiments was run in conjunction with the experiment on light intensity, and seedlings were subjected to the same harvest procedure (512).

Effect of different levels of soil water:

On 27 September 1962, newly-germinated seedlings raised at Lincoln from the same provenance (Lake Pearson) were planted in 8" porous pots containing equal parts of loam, sand and sterilised compost, but no

added nutrients. Seedlings were then placed in the unheated greenhouse until required.

On 18 October, 8 groups each of 4 plants were matched by eye. One group was harvested immediately and the remainder were assigned at random to the following 3 levels in a copper-lined, wooden tank in the unheated greenhouse (figure 5,3).

- (1) 2 groups with the bottom of the pots above the water surface - dry treatment.
- (2) 2 groups with the water surface half-way up the pots - semi-immersed.
- (3) 3 groups with the water surface level with the soil surface in the pots - immersed.

At regular intervals plants were watered at the surface, re-randomised, and sprayed with fungicide to discourage powdery mildew. One group from each treatment was harvested on 20 November, and the other on 18 December. In addition, on 20 November one group was transferred from the immersed to the dry treatment - Dry (2) - and harvested also on 18 December.

Throughout the experiment the soil in the dry treatment was kept moist but freely drained. The soil above the water surface in the semi-immersed treatment rapidly drew up water by capillary action and thereafter remained very moist, if not soggy, whereas the immersed soil was continually saturated and, as its odour testified, was obviously an anaerobic environment.

Table 5,11 shows the average yields at each harvest.

Table 5,11. Average weight (mgm) and leaf area (cm²) of plants at different levels of soil water.

Treatment Harvest	Immersed		Dry(2)		Semi-imm.		Dry	
	18/10	20/11	18/12	18/12	20/11	18/12	20/11	18/12
No. surv. plants	4	4	4	4	4	4	4	4
Total weight	56.6	153.6	698.7	1259.2	549.9	2346.0	671.5	4677.1
S.E.	-	-	76.0	330.0	-	488.9	-	290.1
Leaf area	4.0	11.6	35.8	60.8	48.8	111.9	50.7	174.0
S.E.	-	-	4.3	7.0	-	18.7	-	10.5

Note: standard errors are given for the final harvest only.

The total plant weight and leaf area rose from the initial (18/10) to the final harvest in all treatments, with the greatest increase occurring in the dry treatment. As the data from the intermediate harvest show, plants reacted sharply to full immersion, but there was no significant difference between the dry and semi-immersed treatments. At the final harvest, however, the latter plants had produced only half the yield of dry plants. Even so they grew surprisingly well considering the restricted volume of exploitable soil, but proved to be more variable in their response. This is indicated by the relative size of their standard errors. Plants transferred from the immersed to the dry treatment reacted sharply to the change in water level, almost doubling the yield of their immersed counterparts in the subsequent 4 weeks.

Table 5,12 shows the relations between the weights of separate plant organs at the final harvest for the 3 main treatments.

Table 5,12. Average weights and ratios of separate plant organs.

- (a) Mean weight of organs on 18/12/62 (mgm)
 (b) Means and standard deviations of individual items.
 (c) Ratio weight of organ/total plant weight (%).

(a)

<u>Treatment</u>	<u>Root</u>	<u>Hypocotyl</u>	<u>Leaves</u>	<u>Stem</u>	<u>Total</u>
Immersed	238.0	35.6	267.0	158.1	698.7
Semi-imm.	841.2	92.2	761.4	651.2	2346.0
Dry	1372.8	97.7	1295.3	1911.3	4677.1

(b)

Mean	817.3	75.2	774.6	906.8
S.D. of items	567.8	34.4	514.2	904.4

(c)

Immersed	34.1	5.1	38.2	22.6
Semi-imm.	35.8	3.9	32.4	27.8
Dry	29.3	2.1	27.7	40.9

As the relative size of the standard deviations show, the stem showed the most response to varying soil water levels. A rise in water level resulted in a marked decrease in the ratio stem weight/total plant weight, and a consistent increase in the proportion occupied by other organs. The hypocotyl, being an early formed organ, responded least of all, and its proportion of the total plant weight decreased as the size of the plants increased.

At the final harvest dry plants were tall and vigorous, with an average of 7 stems reaching a mean total length 85 cm, and bearing an average of 58 green, healthy leaves. They also had developed robust

root systems which were freely-branched, abundantly supplied with root hairs, and well distributed throughout the pots. Immersed plants, on the other hand, were structurally weak and monaxial, reaching a mean total height of 19 cm and bearing an average of 13 leaves. The uppermost leaves were green and healthy, the middle ones were distinctly chlorotic, mottled and brittle, while the lowermost ones (1-5) had abscised. The stems and middle leaves were stained with anthocyanin. The root system of immersed plants was confined to the top 3" of soil and consisted of short, thick, main roots which had put out sparsely-branched rootlets devoid of root hairs. An examination at the intermediate harvest showed that the original system had died, probably due to water-logging, and new roots had arisen directly from the proximal end of the tap root. Because of the soft, water-logged soil, the new roots were straight and smooth, and it was evident that the proportion of coarse roots (0.5-1 mm) to fine rootlets (0-0.5 mm) was greater among the new roots (0.55) than in the original system of the initial harvest (0.07). The most vigorous were those near the surface.

The following values, also from the intermediate harvest, compare typical main roots of a dry and of an immersed plant, sectioned 7 cm behind the tips.

Table 5,13. Comparative anatomical measurements of roots (mm).

<u>Treatment</u>	<u>Dry</u>	<u>Immersed</u>
Total diameter	0.68	1.26
Width of cortex	0.21	0.50
Width of primary stele	0.12	0.22
Max. depth of secondary xylem	0.03	+

The immersed root was thicker and characterised by a wider cortex containing much larger cells, a larger primary body, more undifferentiated tissue, and delayed secondary growth. The most striking feature of immersed plants, however, was the remarkable hypertrophy of the lower portion of the hypocotyl and the upper part of the tap root, and the proliferation of loose, cortical tissue.

Plants in the semi-immersed treatment were intermediate in most respects. Their root system was confined to the top 4" of soil, with a dense mat of rootlets at the soil surface.

Those plants transferred from the immersed to the dry treatment were vigorous and healthy at the final harvest. Surviving portions of the original root system had sent forth new rootlets, and the roots formed under immersed conditions grew vigorously. The roots became better distributed throughout the pots, and their youngest portions bore root hairs. The abnormal epidermal and cortical tissue was being obliterated by the growth of normal secondary tissue over it.

These results confirm the observations of Shanks and Laurie (1949b) on Better Times roses subjected to different soil moisture levels. It appears that the effects produced by high soil-water levels are due to poor root aeration acting directly upon the plant.

Effect of soil porosity:

An experiment to study the effects of soil porosity on seedling growth was carried out in the unheated greenhouse in 1962. Newly-germinated seedlings from the same source as in the previous experiment were planted in 8" porous pots on 28 September. One set of 8 pots

contained compacted, Temuka heavy silt loam (12 lbs/pot), and the other set contained a 2:1 mixture of Temuka heavy silt loam and expanded perlite ($6\frac{1}{2}$ lbs/pot). All plants were sprayed with fungicide and watered at frequent intervals, and were harvested on 29 December. One plant in the porous treatment was badly affected by powdery mildew and is not included in the results shown in Table 5,14. It was also found that the roots of 3 plants in the compact treatment had penetrated to the sides and bottoms of the pots. Two of these which showed the greatest response were also eliminated from the final analysis, which must therefore be treated with some reserve as a first indication.

Table 5,14. Average dimensions and ratios of plants in experiment on soil porosity.

- (a) Average dimensions of plants on 29/12/62 (mgm and cm^2).
- (b) Ratio treatment means porous/compact.
- (c) Ratio weight organ/total plant weight (%).

(a) <u>Treatment</u>	<u>N</u>	<u>Roots</u>	<u>Weight of Hypocotyl</u>	<u>Leaves</u>	<u>Stem</u>	<u>Total Weight</u>	<u>Leaf area</u>
Porous	7	546.9	54.5	976.3	443.8	2021.5	140.8
Compact	6	311.6	30.5	559.4	246.4	1147.9	83.3
S.E. of diff.		NA	NA	NA	NA	300.2	16.7
P						< 0.02	< 0.01
(b)		1.75	1.79	1.74	1.80	1.76	1.69
(c)							
Porous		27.1	2.7	48.3	21.9		
Compact		27.1	2.7	48.7	21.5		

NA = Not analysed.

Growth was significantly better in the porous treatment, with plants yielding more than half as much again as those in the compact treatment. As the ratios indicate, all plant organs appear to have been affected equally by the treatments.

It is well known that soil compaction results in an increase in bulk density which in turn means less total pore space and more resistance to root penetration, a low oxygen content, and a restricted movement of water. An examination of the roots from the compact treatment revealed the following features which contrasted sharply with those from the porous treatment:

- (1) Weak development of root crown.
- (2) Reduction in number of main roots.
- (3) Reduction in diameter of roots and rootlets.
- (4) Flattening of roots and rootlets.
- (5) Reduction in number and persistence of root hairs.
- (6) More undifferentiated tissue.
- (7) Delayed differentiation of vascular tissue.

These observations suggest that mechanical restriction and poor oxygen supply were the main causes for lower yields. Shanks and Laurie (1949c) observed similar features in the roots of Better Times roses grown in low concentrations of oxygen.

Effect of exposure:

An experiment on the effect of exposure on the growth of seedlings was carried out in 1962-63. On 26/10/62 seedlings raised at Lincoln in connection with the previous experiments were planted in 6" porous pots containing equal parts of loam, sand and sterilised compost, but no added

nutrients. Seedlings were then placed in the unheated greenhouse until 23 October by which time they had 4-5 leaves. Two sets each of 8 plants were then matched by eye. One set was placed outside in a low-walled cold frame - sheltered treatment, the other was installed in the open on the potting shed roof, about 20 feet above ground level - exposed treatment. Strong northwest winds were blowing at the time and at subsequent intervals during the experiment and this may be assumed to have been the predominating effect. Both treatments were watered frequently and periodically sprayed with fungicide.

The exposed treatment was examined carefully each day during the first 2 weeks to see whether any mechanical damage had occurred, but none was observed. Both treatments were harvested on 3/1/63, and the results are shown in Table 5,15.

Table 5,15. Average dimensions and ratios of plants in experiment on exposure.

- (a) Average dimensions of plants on 3/1/63 (mgm and cm²).
 (b) Ratio treatment means exposed/sheltered.
 (c) Ratio weight organ/total plant weight (%).

(a) <u>Treatment</u>	<u>N</u>	<u>Roots</u>	<u>Weight of</u>			<u>Total</u>	<u>Leaf</u>
			<u>Hypocotyl</u>	<u>Leaves</u>	<u>Stem</u>	<u>weight</u>	<u>area</u>
Exposed	8	1407.6	71.8	821.6	547.1	2848.1	82.2
Sheltered	8	1251.2	58.5	817.2	512.8	2639.8	88.3
S.E. of diff.		NA	NA	NA	NA	378.8	12.8
P						NS	NS
<hr/>							
(b)		1.12	1.23	1.01	1.07	1.08	0.93
<hr/>							
(c)							
Exposed		49.4	2.5	28.8	19.2		
Sheltered		47.4	2.2	31.0	19.4		

NA = Not analysed.

Exposed plants gave a slight increase in total yield and a decrease in leaf area, but the differences are not significant. As the ratios in (c) show, the roots and leaves were the most affected organs on a dry weight basis. Although the evidence provided by such a small number of plants is rather tenuous, the conclusion to draw is that the assimilates have been differently employed. In exposed plants the trend seems to lie in the direction of an increase in the proportion of root to shoot, though to some extent this tends to be offset by an increase in the number of secondary stems and many more leaves.

The changes in morphology brought about by exposure are perhaps more informative. These are given in Table 5,16.

Table 5,16. Comparative morphology of exposed and sheltered seedlings on 3/1/63 (mean values in cm and cm²).

<u>Treatment</u>	No.	Stem			Leaves		
		Total length	Average length stem	Length inter-node	No.	Total area	Area average leaf
Exposed	6.7	51.3	7.6	1.0	51.6	82.2	1.6
Sheltered	5.2	45.6	8.8	1.5	31.1	88.3	2.8
Ratio treat.							
means	1.29	1.12	0.86	0.66	1.66	0.93	0.57

Exposed plants had more but smaller stems and leaves than sheltered plants. They were also smaller; the mean length of the main stem was 12.4 and 17.0 cm respectively. Other contrasts are indicated in the following list which summarises all the consistent features associated with exposure.

- (1) Reduction in height - dwarfing.
- (2) Precocious development of axillary buds - bushiness.
- (3) Small leaves (compensated by an increase in number).
- (4) Increased proportion of root.
- (5) Increased number and persistence of root hairs.
- (6) Increased hairiness and folding of leaflets.
- (7) Thickening of cell walls and reduction in intercellular spaces.
- (8) Presence of anthocyanin.

All these changes point in one direction, namely an increase in xeromorphy, due to continual exposure to drying winds. According to Whitehead (1963), the main effect of wind is to reduce the water balance of the plant (in this case by excessive loss) even if the roots are in optimum conditions for water uptake. Continual loss of water upsets the processes of differentiation, but only in extreme cases is the photosynthetic apparatus itself affected. Whitehead considers that essentially similar morphological and anatomical changes are produced by adverse soil moisture conditions, though this view has been seriously contested (Humphries and Roberts, 1965).

In this experiment the increase in xeromorphy brought about by exposure may be looked upon as an advantage in reducing excessive water loss, while at the same time maintaining the same (or even better) rate of photosynthesis as judged by dry weight. One further comment should be added. The contrasts evident under two extremes of exposure are essentially the same as those produced in contrasting light environments. This emphasises an earlier assertion (511) that in this study the light climate is regarded as a complex of interdependent factors, and indeed in

this experiment more than one factor will have been affected by the treatments employed.

523. Discussion

In the field sweet brier seedlings can be seen in a number of habitats on many soil types (521). They are capable of surviving, although not necessarily thriving, under extreme conditions of soil dryness, waterlogging, soil compaction, and exposure that would kill off most other shrub seedlings. However, they will not survive indefinitely and the weaker ones will ultimately succumb. Desiccation of seedlings on dry sites and heavily compacted soils was frequently observed (721), as also was the chlorotic appearance and ultimate death of seedlings subjected to prolonged water-logging. If conditions change, these subdued seedlings often recover (522). It appeared that the high initial rate of seedling survival was associated closely with the inherent ability of the plant organs, especially roots, to adapt themselves to such extremes.

Experiments on the relations of sweet brier seedlings to different conditions of soil aeration and soil water levels confirmed their phenotypic plasticity, and proved that they have a strong resistance to extremes of habitat. Decreasing soil aeration and permeability, or prolonged water-logging, prevents the development of a normal root crown (461) resulting in poor top growth and the differentiation of morphological and anatomical characters peculiar to each treatment. Poor soil aeration (porosity) acts indirectly on the root system through its effect on soil properties, whereas poor root aeration (water logging) acts directly upon the plant.

Experiments on exposure showed that no mechanical damage occurred and that the main effect of wind was to reduce the water balance without apparently upsetting the photosynthetic apparatus. Seedlings subjected to continual exposure show a tendency to develop a greater ratio of absorptive to transpiring surface, and pronounced xeromorphy in their morphology and anatomy.

It is concluded that sweet brier seedlings are probably better adapted than most shrubs to adverse habitats. The morphological and anatomical changes which result from poor air and water relations produce a phenotype which can survive where other shrub seedlings would die. Although it may be argued that such changes are obligatory and that any species will produce them if subjected to similar conditions, this plasticity of sweet brier seedlings is nevertheless an important feature in establishment.

Since it is assumed that the behaviour of seedlings shows the same relations to these conditions as older plants, the experimental results have some applicability to established sweet brier in the field. The ideal air and water relations for seedling growth imply optimum conditions for later growth of mature plants. The ideal medium for good growth should provide:

- (1) Good internal and surface drainage.
- (2) Optimum supply of air and water.
- (3) Good root penetrability.

SECTION 3. (531) SOIL FERTILITY

Information on the nutritional requirements of roses in general is surprisingly meagre considering their cultural and commercial importance. In general the leaves of roses contain a greater amount of mineral ash in proportion to their dry weight than many other shrubs, and this is usually accepted as an indication of higher fertility demands.

Of the major elements considered essential for plant growth, nitrogen (N), phosphorus (P), potassium (K), and calcium (Ca) have received the most attention from investigators. Shanks and Laurie (1949a) tested the separate effects of N (NaNO_3), P (NaH_2PO_4), K (KCl), and Ca (CaCl_2) on the growth of Better Times roses over 4 months in a greenhouse, and found that the order of relative importance for top and root growth appeared to be N P Ca K. An interesting feature of their work which somehow escaped comment was the 3-fold increase in yield obtained with monammonium phosphate ($\text{NH}_4\text{H}_2\text{PO}_4$), suggesting a significant PN interaction. Laurie and Kiplinger (ex Culbert and Wilde, 1948) suggest an optimum range of 10 - 25 ppm of N, 5 ppm of P, and 20-40 ppm of K, based on a Spurway soil extract. Chan (1960) considers that the following nutrient levels are required for good growth of roses: N at 2.8 - 3.0 %, P at 0.28 - 0.30%, and K at 2.4 - 2.6%. An interesting observation is that of Seeley and Davidson (1940), who found that Briarcliff roses appeared to require relatively high amounts of P, depending on the concentration of other nutrients present.

No separate experiment was run to determine the individual effects of different nutrients on the growth of sweet brier seedlings. This aspect was covered to some extent in a factorial experiment in which

soil fertility, soil moisture, and plant competition were studied together (see Section 4). However, since the yields of seedlings growing in the absence of competition in this experiment were so much larger than those subjected to competition, they were taken out and analysed separately.

Table 5,17 shows the yields obtained from seedlings grown under moist and dry soil conditions in native soil which, from the agricultural viewpoint, is known to be deficient in N, P, sulphur, and molybdenum. This soil and the experimental procedure are described in 541 and 542.

Table 5,17. Average dry weight (gm) of seedlings grown in Tekapo soil

<u>Fertiliser applied</u>	Shoots	
	<u>Moist treatment</u>	<u>Dry treatment</u>
Nil	5.2	1.9
NPS	19.6	4.8
PN	17.0	4.0
PS	13.1	3.9
NS	1.7	1.0
P	3.3	4.9
S	3.4	1.7
N	1.9	1.2
Roots 0 - 8 cm		
Nil	0.8	0.4
NPS	3.8	2.0
PN	4.4	1.8
PS	1.9	0.7
NS	0.3	0.2
P	0.7	1.4
S	0.8	0.3
N	0.4	0.1

Note: weight of roots is expressed in gm/685cc, the volume of soil taken.

In the table, substantial differences in yield are shown according to the fertiliser elements applied. These remain fairly constant irrespective of soil moisture, except in the P-alone moist treatment. As it turned out, this box was poorly located in the experimental design, receiving less direct light in comparison with other boxes (border effect). Had this box been more favourably located, then the growth of seedlings would have been much better.

The important points in Table 5,17 insofar as seedling growth is concerned are:

- (1) A response to P, particularly in shoot growth.
- (2) A response to N only in the presence of P.
- (3) A depression to N alone.
- (4) No response to S.

It appears that the level of N in untreated soil is fairly adequate for growth, providing the deficiency of P is corrected.

These data combined, together with the yield of roots 12 - 20 cm, were tested for significance using Duncan's Multiple Range Test, and the results are given in Table 5,18. In the table, treatments with letters in common do not differ significantly: lower case letters indicate 5% level, upper case letters, 1% level. It is important to note that the Duncan letters refer only to differences between treatments (e.g., No P, P), not the column as a whole.

Table 5,18. Dry weight (gm) of seedlings grown in Tekapo soil.

<u>Treatments</u>	<u>Weight of shoots</u>	<u>Weight of roots 0 - 8 cm</u>	<u>Weight of roots 12 - 20 cm</u>
No P	18b	0.8bB	0.14b
P	70a	4.2aA	0.44a
No S	39a	2.5a	0.29a
S	49a	2.5a	0.28a
No N	37a	1.7a	0.36a
N	51a	3.3a	0.21a
Dry	23b	1.7a	0.29a
Moist	65a	3.3a	0.28a
C.V. %	65.6	54.7	68.6
Significant 5% interactions	-	P X N	-
1%	-	-	-

Note: significant interations are given in Appendix 5,1.

Both shoots and roots responded to increments of P. Shoot growth was also much better when the roots were in moist soil conditions. Although the differences in yield are substantial for P, N, and the main effect of moist vs dry, they did not exceed the 5% level, except in roots 0 - 8 cm with and without P. It is obvious that treatments varied considerably as the high coefficients of variation suggest. The principal variation lies in the low yield of roots, which tends to raise the C.V., and the inherent difference in branching habit - some plants became very bushy, while others were sparingly branched. The C.V. could have been reduced had it been possible to increase the replication (see figure 5,3). The average height of seedlings was found to be less variable and a more reliable measurement (table 5,23).

The P X N interaction was some distance from significance on yield of shoots, and quite negligible on roots 12 - 20 cm. There was a positive interaction at the 5% level on roots 0 - 8 cm.

These results show that P is the most limiting major element for seedling growth in Tekapo soil. From the agricultural viewpoint, most of our native soils are deficient in P. The major exceptions as far as sweet brier is concerned are the soils of drier regions where the organic cycle is weak and losses of P from the soil by leaching are minimised, and recent or rejuvenated soils in which mineralisation has occurred and there is a higher percentage of available inorganic P in proportion to the total P content (313).

Walker (1964) who has examined the relative availability of P in various soil sequences throughout New Zealand, stresses the great ecological significance of the element and its importance in pedogenesis. Beadle (1954) also presents data which indicate that soil phosphate may play an important role in delimiting plant communities in eastern Australia. From field observations it appeared that many of our native soils fail to satisfy the requirements of sweet brier. The present and subsequent experiments indicate that phosphate is largely concerned.

SECTION 4. COMPETITION541. Description

This section extends the discussion of factors affecting seedling growth to the final and perhaps most important factor of all, namely plant competition. Earlier (313) it was noted that sweet brier prefers open habitats where there is a reduction in herbaceous vegetation attended by a decrease in competition, thus enabling the more deeply rooted sweet brier to get started and survive.

It is difficult in the field to establish experimentally the factors involved in competition. However, by choosing an infertile native soil and varying its fertility, moisture, and cover, the problem of whether different levels of fertility and moisture affect sweet brier directly through growth stimulation, or negatively through competition from the stimulated cover can be studied. Thus, a greenhouse experiment was designed to study competition between sweet brier, grass, and clover seedlings.

Soil:

The soil used was obtained from an out-wash terrace at 2,100 ft near Lake Coleridge, Rakaiia catchment, known locally as "1,000 acre flat", which receives c. 33" rainfall yearly. Between 500 and 1,000 years ago it supported continuous forest dominated by mountain beech (Nothofagus solandri var. cliffortioides). It now grows a humid form of short-tussock (Festuca-Poa) grassland, but isolated plants of snowgrass (Chionochloa rigida) testify to a previous tall-tussock community prior to the advent of Europeans. A list of present plants and their frequency is given in Appendix 5,2.

The soil is classified in the Tekapo set, which is a dry-hygrous Upland and High Country Yellow Brown Earth, usually developed on rolling land and hills. It is not a typical Tekapo soil, however, and is more likely to belong to the Craigieburn set, a hygrous U. and H.C. Y-B-E, usually developed on terraces. The A horizon consists of 6" of dark brown silt loam, with a friable, weakly developed crumb structure, and many roots. The B horizon consists of c. 7" of yellowish brown, slightly sticky silt loam with stones, with a very weakly developed fine crumb structure, and few roots. This in turn overlies a strong brown stony silt loam, merging to greywacke stones and boulders. The physical condition and nutrient status of this soil is shown in Table 5,19.

Table 5,19. Physical and chemical analysis of Tekapo soil.

Depth (in.)	pH	Quick tests*			Total C %	Total N %	C / N
		Ca	K	P			
0-7	5.1	2	7	1	4.28	0.23	19

Depth (in.)	C.S. %	F.S. %	Silt %	Clay %	Spec. gravity	Moist. equiv. %	Bulk density
0-7	1.7	41.9	29.6	26.8	2.49	37.1	0.68

* The indices used in quick tests are given in Appendix 5,3.

Like most ex-mountain beech soils, this soil is strongly leached, low in bases, and responds to N, P, S, and Mo (531). Its moisture holding capacity is good, but the soil is light and is easily dried out.

Fertiliser:

The nutrients varied in this study were N, P, and S. A basal dressing of Mo at the rate of 5oz/acre was applied to all treatments.

Nitrogen as urea (46%N) was applied at the rate of 200lb N/acre; phosphorus as "ibex" double superphosphate (56% P₂O₅ or 24.8% P) at the rate of 58.8lb P/acre (equivalent to 6 cwt 44/46 superphosphate per acre); and sulphur as gypsum (19.2% S) at the rate of 20lb S/acre.

Plant material:

The sweet brier seedlings used were progeny of N type brier seed collected from Lake Pearson in 1960/61, and sown in connection with germination experiments. The two grass species used were sweet vernal (Anthoxanthum odoratum) and brown-top (Agrostis tenuis) obtained from commercial lines drawn from Southland and Canterbury respectively. These species were chosen because of their ecological significance in sweet brier populations. The clovers used were white clover (Trifolium repens) and red clover (T. pratense) obtained from pure commercial lines. These species were chosen because of their significant role in the improvement of pastures infested with sweet brier.

Related studies:

The effects of competition among grasses and shrub seedlings have been demonstrated in several countries. The chief findings of American workers are summarised by Gartner, et al (1957) and Johnsen, (1962). It appears that when grasses and shrub seedlings are growing together there is a negative correlation between the foliar density of herbaceous vegetation and the number and vigour of shrub seedlings. Artificial seeding of herbaceous species affords adverse growing conditions to shrub seedlings. Most workers report a competitive effect among root systems. It is well known that soil moisture is depleted by a mat of fibrous grass roots, and it is generally concluded that shrub seedling mortality in

drier areas is largely a matter of competition for soil moisture.

The effects of fertilisers on the tops and roots of cultivated plants is fairly well known. Likewise, the competition among crop and pasture plants has been studied intensively (Donald, 1963).

Several studies have been made on the response of short-tussock grassland to applied fertilisers and artificial seeding. O'Connor (1961), working on a similar soil (Craigieburn set) to the one chosen for this study, found that resident grasses (including brown-top and sweet vernal) were suffering from serious nutritional deficiencies which were not confined to N, but included P and S. He found that the addition of P and S made possible a further response by grasses to applied N, and the introduced grasses were more responsive than native grasses in this respect. His work also indicated that browntop may be less demanding for, or superior in obtaining, P and S than sweet vernal, and that both were superior to native vegetation in their ability to draw on nutrients in short supply. This indicates the strong competitive powers of these two species.

As far as I am aware, the effects of applied fertiliser on shrub seedlings in this country have not been studied.

542. Experimental procedure

On 22 May, 1962 soil was excavated from the 0-7" depth at "1,000 acre flat". This depth corresponded to the A horizon and the transitional zone between it and the B horizon. Enough soil was brought back to Lincoln where it was shredded, and most of the coarse roots of sub-shrubs were removed. In June, screened soil was put into 64 boxes, each 3ft deep with inside dimensions of 15" x 15½", giving a total surface area of c. 1/26900 acre. About 5" of river-washed gravel and sand was placed in the bottom of each box to assist drainage, and a given amount of soil of known moisture content was tamped into each box so that the bulk density approximated that obtained in the field (post-harvest measurements of 3 boxes selected at random averaged 0.64 bulk density compared with 0.68 for undisturbed soil). The boxes were then placed in position in an unheated greenhouse. Each box was surrounded by a narrow layer of sawdust to prevent moisture loss, and the entire experiment was surrounded with a 6" layer of sawdust held in place by light wooden framework and scrim (figure 5,3).

Newly-germinated seedlings of sweet brier were transplanted in September to shallow flats containing untreated Tekapo soil. Seed of the two grass species was sown in other flats to raise adequate stocks of seedlings. All seedling stocks were placed in an unheated greenhouse until required.

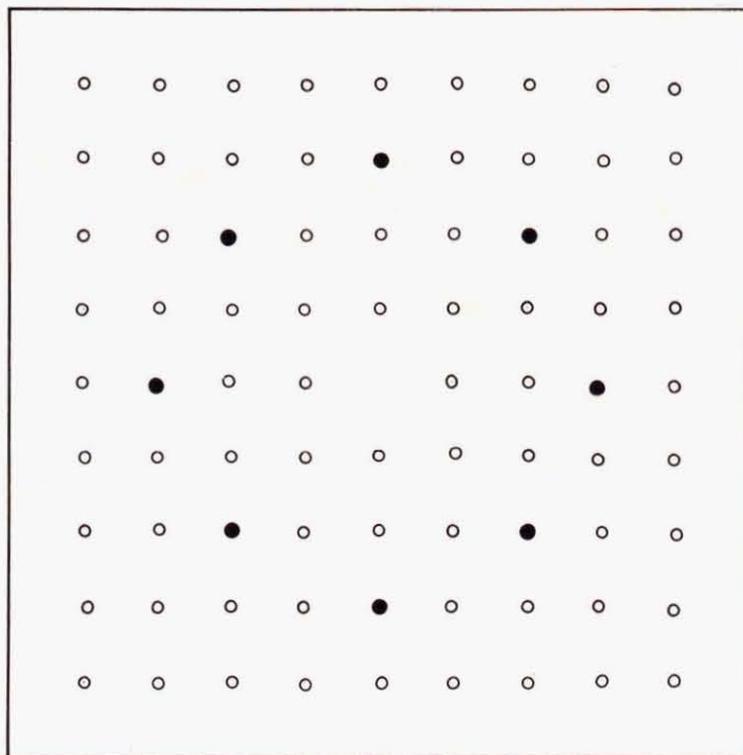
Before planting, soil fertility was varied by mixing fertiliser elements into the top 3" of soil in each box. The 8 combinations applied were P, N, S, O (nil), NS, PS, PN, and PNS.

Fig. 5,3.

General view inside the unheated greenhouse, showing the experiments on different water levels, and competition.

Fig. 5,4.

Diagram showing the relative positions of grass and sweet brier seedlings in boxes in the competition experiment.



● Sweet brier

○ Grass

Between 11 and 15 October, 36 browntop and 36 sweet vernal seedlings about $1\frac{1}{2}$ " tall were planted at random at $1\frac{1}{2}$ " centres in systematic rows in grass only and grass plus clover boxes. At the same time, 8 sweet brier seedlings at the 3-4 leaf stage were planted in systematic positions within each box (figure 5,4). One week later, inoculated clover seed was broadcast in grass plus clover boxes.

Two cutting combinations were applied to grass alone boxes; in one the grass was left uncut throughout the experiment; in the other it was cut back to about 1 inch when cover in the best boxes had outgrown sweet brier seedlings. All grass plus clover boxes were cut back also. Sweet brier was not cut until the final harvest. All boxes were watered frequently by hand until 27 December, by which time seedlings were well established. After this, water was withheld from half the boxes until seedlings showed signs of wilting. These were then allowed to recover by light watering only.

Thus, the entire experiment consisted of 64 boxes of one soil type, 8 levels of nutrients, 3 cover and 2 cutting combinations, and two levels of soil moisture. The experiment was a single replicate of a 4×2^4 factorial design, arranged in blocks of 16, confounding the main effect of "moist vs dry" and part of the 4-factor interaction between "grass x P x N x S".

The experiment ran from 15 October 1962 to 27 February 1963. Daytime temperatures ranged from 18° to 35°C , sometimes exceeding 38°C , and night temperatures varied between 5° and 12°C . Relative humidities were high, especially at night ($> 90\%$). All boxes were frequently sprayed with fungicide to combat powdery mildew on sweet brier.

At certain intervals (3/12/62, 27/12, 25/1/63) growth of sweet brier seedlings was measured and grass and clover were harvested, oven-dried, and weighed. The outside row of grasses was excluded from the analysis. At the final harvest (27/2/63), the tops of all seedlings were harvested, measured, and oven-dried. Two large soil cores (685 cc) were taken vertically over the cut stumps of 2 sweet brier seedlings at 0-8 cm and 12 - 20 cm in each box. Where applicable, roots of sweet brier and other species were separated in a root washing apparatus, each was oven-dried and weighed, and average weights were calculated.

After this, a side of each box was removed and soil samples were taken with a sampling tube at various depths to determine differences in soil moisture, and whether any significant shift in pH had occurred (figure 5,5).

543. Results

Grass and clover growth:

Grass plants grew well after planting, their vigour varying according to level of fertility. They were uniform as seedlings, and only a few replants were needed during the first 2 weeks. Unfortunately, the clovers established poorly, and although a second broadcast was made, most seedlings died through exposure to high temperatures at the soil surface or damage to their radicles from excessive fungicide. Better establishment was achieved in boxes receiving amendments of S; a result in accord with field trials on soils of this type. The clover plus grass treatment seemed to be more effective than grass alone (cut) in suppressing brier growth, but it probably shows more significant differences than are warranted.

The relative growth of grass and grass plus clover in the cut treatments is given in Table 5,20. Data from the first 3 harvests only are included. These and subsequent data in this experiment were analysed using Duncan's Multiple Range Test. The interpretation of this test is described elsewhere (531).

Table 5,20. Mean dry weight (gm) of grass and grass plus clover tops at three harvest dates.

<u>Treatment</u>	<u>1st harvest</u> <u>3/12/62</u>	<u>2nd harvest</u> <u>27/12/62</u>	<u>3rd harvest</u> <u>25/1/63</u>
Cut grass	7.7a	7.1a	8.7a
Cut grass/clover	7.9a	7.2a	6.5b
No P	0.7bB	4.7bB	8.0a
P	14.9aA	9.6aA	7.3a
No S	7.8a	7.4a	8.0a
S	7.9a	6.9a	7.2a
No N	1.8bB	5.2bB	7.7a
N	13.8aA	9.2aA	7.5a
Dry	8.1a	7.4a	5.8b
Moist	7.6a	7.0a	9.5a

Significant interactions	5%	Sx moisture	Sx grass, PxN Sx moisture	P x N N x moisture
	1%	P x N	P x S	-

Note: significant interaction tables are given in Appendix 5,4.

There were no differences in yield between the grass treatments, except at the third harvest. There was also a significant depression of grass yield after the moisture stress had been applied. The most important result, however, was the large initial response to P and N separately, and the substantial increase in yield when P and N were acting

together. By the third harvest there was very little response to P and N separately, and the interaction was negative. The only explanation I can offer for this is that after a rapid flush of growth the nutrient supply became depleted. Also, it is known that frequent, heavy defoliation of grasses slows down root development. Thus the ability of plants to draw on nutrients is lessened and yields decrease.

The other interactions are more difficult to interpret. The indications are that there is a tendency to an N depression and an S response in dry soil.

In Table 5,21 the yield of all grass treatments up to and including the fourth and final harvest is considered.

Table 5,21. Dry weight (gm) of grass and grass plus clover roots at the final harvest, and total dry weight of tops for 4 harvests.

<u>Treatment</u>	Weight of roots 0 - 8 cm	Weight of roots 12 - 20 cm	Total grass tops (4 harvests)
Cut grass	3.5bB	0.9bAB	32bB
Cut grass/clover	3.3bB	0.7bB	28bB
Uncut grass	6.4aA	1.4aA	53aA
No P	4.2a	0.9a	24bB
P	4.6a	1.0a	51aA
No S	4.4a	0.9a	38a
S	4.4a	1.1a	38a
No N	3.8b	0.8b	28bB
N	5.0a	1.1a	48aA
Dry	4.6a	1.2aA	31bB
Moist	4.2a	0.7bB	44aA
C.V. %	38.2	55.6	30.7
Significant interactions	5% 1%	- -	- S x N
			Grass x P x N P x Grass, P x N, Moisture x grass

Fig. 5,5.

A dismantled box from the competition experiment, showing the sampling positions for post-harvest soil moisture (left) and pH (right).

Fig. 5,6.

Dismantled boxes from the competition experiment, showing the extent of grass roots.

Left = grass x NPS x dry

Right = grass x NPS x moist

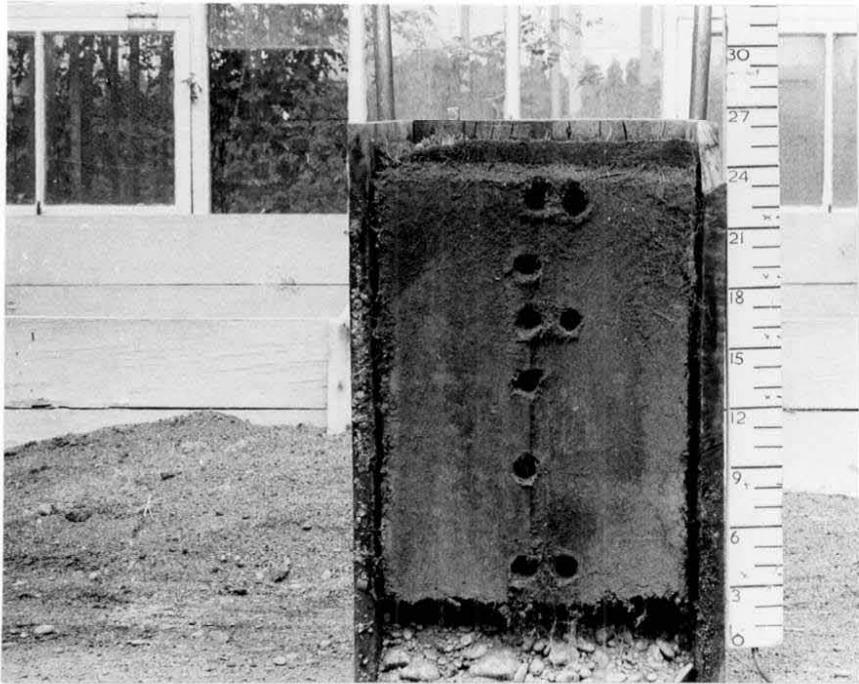


Table 5,21 (cont.)

Note: significant interaction tables are given in Appendix 5,5.

Frequent defoliation of grasses resulted in a significant reduction in root weight and total yield of grass tops. Dry soil conditions also reduced the yield of grass tops, but the weight of roots increased significantly at deeper soil levels (figure 5,6). As the interaction tables show, the tops of uncut grass were strongly affected by soil dryness, and the roots of all grasses responded to increments of N and S together. These effects are well known in native soil of low nutrient content. However, as in the previous table, the most important feature in grass growth is the large response to P and N separately, and the strong positive interaction of both together. The deficiency of P in this soil is emphasised by the response of both cut and uncut grass to increments of this element (Appendix 5,5).

Sweet brier growth:

Most sweet brier seedlings growing with grass survived to the final harvest. One or two died in uncut grass boxes, and two plants in a cut grass box were eaten by the tomato worm, Heliothis armigera. At the final harvest, seedlings growing in the absence of grass varied in size and vigour according to level of fertility and soil moisture. As stated previously, their yields were much greater than in grassed boxes (figure 5,7) and they were analysed separately (531). In the following table the yields of seedlings growing with grass are presented.

Fig. 5,7.

Relative growth of sweet brier seedlings in the
competition experiment.

Treatments:

Down: no grass x moist.
cut grass + clover x moist
uncut grass x moist

Across: NS, PS, PN, PNS



Table 5,22. Dry weight (gm) of sweet brier seedlings growing in competition with grass and clover.

<u>Treatment</u>	Weight of <u>shoots</u>	Weight of roots <u>0-8 cm</u>	Weight of roots <u>12-20 cm</u>
Cut grass	2.8aA	0.21aA	0.02a
Cut grass/clover	1.8abAB	0.19aA	0.02a
Uncut grass	0.7bB	0.08bB	0.01a
No P	1.9a	0.17a	0.02a
P	1.5a	0.15a	0.01a
No S	1.8a	0.17a	0.01a
S	1.7a	0.15a	0.02a
No N	1.7a	0.17a	0.02a
N	1.8a	0.15a	0.01a
Dry	1.1b	0.14a	0.02a
Moist	2.4a	0.19a	0.02a
C.V.%	103.9	76.0	114.9
Significant	5%	-	PxS, Nx moisture
interactions	1%	-	-

Note: significant interaction tables are given in Appendix 5,6.

The data in this table, compared with those in Table 5,18, clearly demonstrate the marked reduction in growth of seedling brier in the presence of grass, particularly when the grass is left uncut and develops a thick mat of fibrous roots, and a dense canopy of leaves. As expected, this suppression is reinforced under dry soil conditions. Root growth of seedling brier was severely restricted by the presence of grass roots irrespective of fertility or soil moisture levels. The root system of these seedlings consisted of a long, thin, and sparsely branched tap root, compared with the freely branched and robust system of seedlings

in no-grass boxes (figure 5,8). This coincided with the thin, monaxial stems above ground level in grassed boxes compared with the multiaxial shoot system in no-grass boxes.

The effect that grass competition had on seedling height is shown in the following table.

Table 5,23. Average length (cm) of the main stem of seedling brier at different grass harvests.

<u>Treatment</u>	<u>1st harvest</u> <u>3/12/62</u>	<u>2nd harvest</u> <u>27/12/62</u>	<u>3rd harvest</u> <u>25/1/63</u>	<u>Final harvest</u> <u>27/2/63</u>
No grass	3.3aA	9.5aA	24.5aA	39.5aA
Cut grass	2.2bB	3.6bB	6.0bB	10.4bB
Cut grass/clover	2.3bB	3.3bB	4.9bB	8.4cB
Uncut grass	2.2bB	3.2bB	4.5bB	5.4cB
No P	1.6bB	3.4bB	7.7bB	14.9b
P	3.3aA	6.4aA	12.3aA	16.9a
No S	2.4a	4.6a	9.5a	15.2a
S	2.5a	5.2a	10.5a	16.6a
No N	2.1bB	4.5a	10.0a	17.0b
N	2.9aA	5.3a	10.0a	14.8a
Dry	2.3a	4.4a	8.5b	12.3bB
Moist	2.7a	5.4a	11.5a	19.5aA
C.V.%	29.3	47.3	49.8	41.1
Significant interactions	5% 1%	- Pxgrass P x N	- Pxgrass P x N	- Pxgrass P x N

Note: significant interaction tables are given in Appendix 5,7.

These results add further support to trends shown by the dry weights. The presence of grass resulted in a significant reduction in the length of the main stem of seedling brier, particularly if the grass

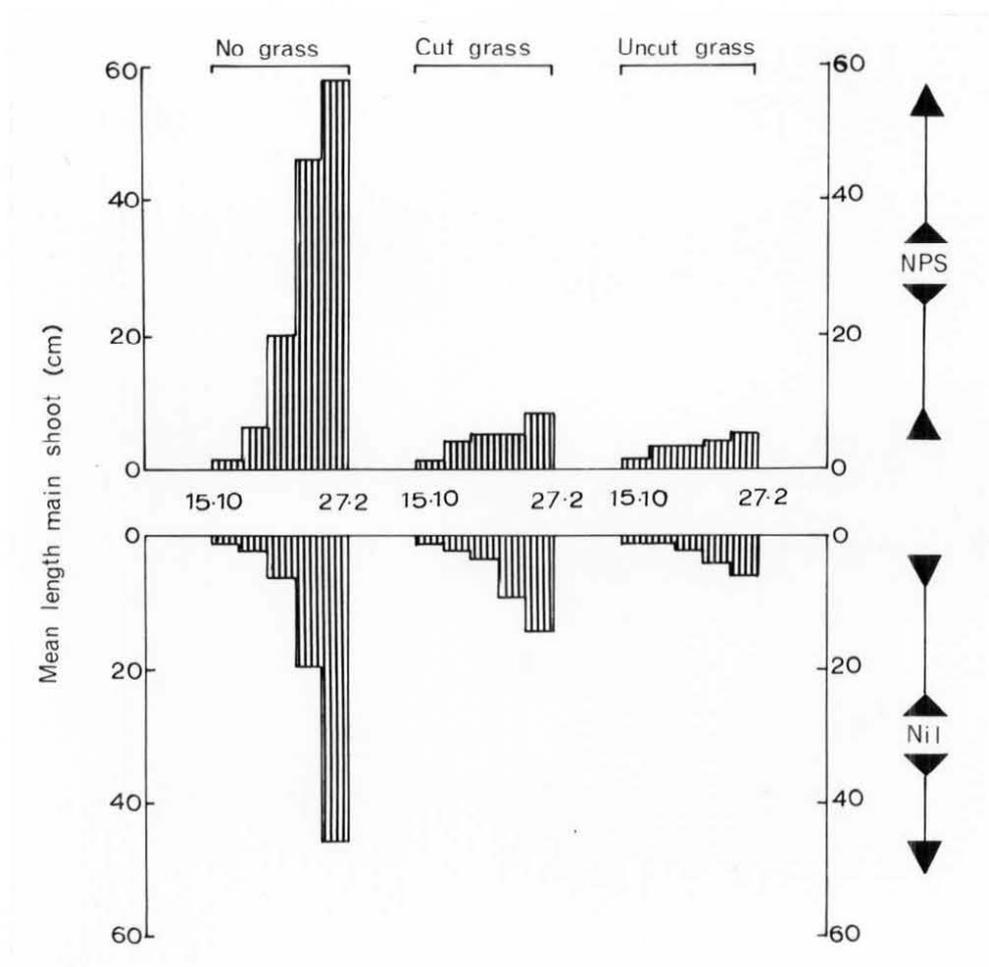
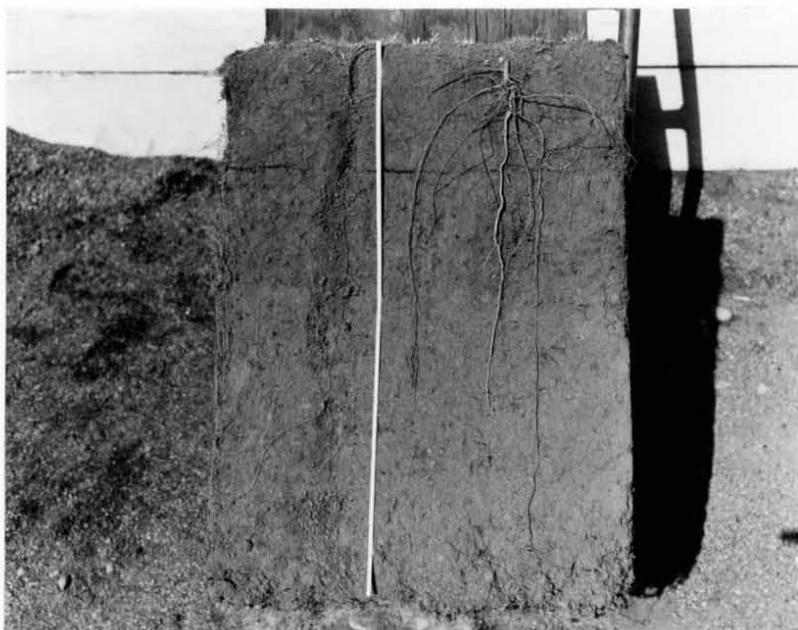
Fig. 5,8.

Contrasting root systems of sweet brier growing with grass (left) and in the absence of grass (right).

Treatments = PNS x dry.

Fig. 5,9.

Effects of grass competition on the mean height of sweet brier seedlings grown in Tekapo soil.



was left uncut and soil allowed to dry out. Throughout there was a large response to P and a positive P x N interaction, but the most significant feature was the consistent P x grass interaction which shows clearly that seedling brier will not grow bigger with added P if grass is present.

Soil moisture:

Post-harvest soil moisture determinations are shown in the following table.

Table 5,24. Post-harvest soil moisture (% by volume) in the competition experiment.

<u>Treatment</u>	<u>Depth (cm)</u>			
	<u>5 - 10</u>	<u>10 - 15</u>	<u>18 - 23</u>	<u>40 - 45</u>
No grass	16.1a	17.3a	14.5a	18.1a
Cut grass	15.8a	16.7ab	16.9ab	17.7a
Cut grass + Clover	16.6a	17.0a	17.3a	18.3a
Uncut grass	15.6a	15.6b	15.8b	16.6a
No P	16.9aA	17.6aA	17.9aA	18.9aA
P	15.1bB	15.7bB	15.8bB	16.5bB
No S	15.9a	16.5a	16.7a	17.5a
S	16.1a	16.8a	17.0a	17.9a
No N	16.4a	17.2a	17.4a	18.3a
N	15.7a	16.1b	16.3b	17.0b
Dry	9.4bB	10.3bB	10.5bB	11.0bB
Moist	22.6aA	23.0aA	23.1aA	24.4aA
C.V.%	13.1	11.4	11.7	13.5
Significant interactions	1% -	P x grass Grass x moisture	P x grass Grass x moist.	P x grass Grass x moist.

Note: significant interaction tables are given in Appendix 5,8.

As expected, there was a significant difference between watering treatments. Grass roots tended to lower the soil moisture at intermediate depths, but did not affect it at shallower or deeper levels. Amendments of P and N also lowered the soil moisture, mainly through stimulated root growth. This effect was most apparent where seedling brier grew alone, more than in uncut grass boxes, and least noticeable where grass and clover were cut and their root growth retarded. As the moisture x grass interaction tables show, uncut grass seriously depleted soil moisture after the normal watering was withheld.

Soil reaction:

It is believed that heavy applications of N (particularly as urea) and S without added P tend to lower the pH and reduce yields. This appeared to be the case in this experiment where depressions to applied S were recorded in moist boxes, and depressions to applied N in dry boxes. Also, the application of N and S together had a general depressing effect on shoot yields. Although this may be attributed to increased soil acidity (Table 5,25), it was more likely caused by an imbalance of nutrients. Unless P is present in adequate amounts, both grass and sweet brier seem unable to take full advantage of increments of N and S separately, or together.

Post-harvest pH determinations are presented in Table 5,25, which shows a significant reduction in pH in the top few cm when N and S were applied, and a reduction at all depths recorded when sweet brier was growing by itself. The cause of the latter is not directly apparent.

Table 5,25. Post-harvest pH determinations in the competition experiment.

<u>Treatment</u>	<u>Depth (cm)</u>		
	<u>5 - 10</u>	<u>18 - 23</u>	<u>50 - 55</u>
No grass	5.13b	5.13b	5.12b
Cut grass	5.21a	5.28a	5.27a
Cut grass + clover	5.16ab	5.25a	5.23a
Uncut grass	5.10b	5.23a	5.26a
No P	5.13a	5.21a	5.19a
P	5.17a	5.24a	5.25a
No S	5.18a	5.22a	5.20a
S	5.12b	5.22a	5.24a
No N	5.19a	5.22a	5.23a
N	5.11b	5.22a	5.21a
Dry	5.12a	5.23a	5.23a
Moist	5.18a	5.22a	5.21a
C.V. %	2.0	1.5	2.2

Note: the pH for undisturbed soil was 5.1 (Table 5,19).

544. Discussion

The above experiment departed from field conditions in the following respects:

- (1) 2 ft of topsoil was used as against a normal soil profile in the field.
- (2) Grass and sweet brier seedlings were sown together. In the field the grass is usually well established by the time sweet brier seedlings emerge.

(3) Lateral development of roots was restricted by the narrow boxes.

(4) Watering schedules, temperatures, and humidity were abnormal.

Although these conditions were artificial, the general principles involved still apply. The results demonstrate that sweet brier, browntop, and sweet vernal respond to added fertiliser in soils where the nutrient supply is low. The main nutrient which this and other native soils lack is phosphorus. There appears to be a strong correlation between the level of available P and seedling size when sweet brier is growing alone, but not when it is growing with grass. When grass is present, there is initially strong competition for nutrients, and secondary effects of competition for soil moisture and presumably light. When moisture becomes a limiting factor, competition is more acute.

Figure 5,9 shows that grass competition accounts for most of the variability in seedling size. The mere presence of grass suppresses the growth of seedling brier irrespective of soil fertility, though the degree of suppression is intensified when the growth of competing grasses is stimulated. When the grass is cut, the young sweet brier plants grow a little better. This may indicate release from light competition, but it should be emphasised that cutting reduces the competitive ability of the grasses by retarding their root growth. Competition for light is probably not important in the establishment of sweet brier in most types of grassland. The principal competitive effect concerns the root systems. Sweet brier seedlings have their roots in the zone of highest grass root concentration and compete directly with grasses for nutrients and soil moisture.

It appears that sweet brier seedlings are certain to show some survivors in most seasons, provided they encounter a suitably moist and reasonably fertile soil, and thin, open vegetation. The frequent cause of seedling mortality and lack of regeneration in current populations is the change to a more dense, competitive cover since the establishment of the original shrubs.

CHAPTER 6

THE MATURE PLANT IN ITS NATURAL ENVIRONMENT

INTRODUCTION

Although sweet brier will grow under a wide range of environment, there is a narrower range within which it performs exceedingly well. Differences in environment can be detected by corresponding changes in number, size, and weight of various plant organs, as well as by certain internal diagnostic features. But the size and vigour of the plants as a whole are equally useful guides to performance.

In this study the following plant attributes were measured: length and width of new basal shoots; width and number of rings in mature shoots; length and fresh weight of fruiting shoots; area of leaves; number and fresh weight of hips per fruiting shoot; volume of hips; number and oven-dry weight of achenes.

Factors of the environment such as rainfall and temperature can be measured, but their individual effects on plant growth in the field are difficult to separate. Combinations of two or more factors are difficult to assess quantitatively. Attempts were made to compare mature plants growing on sites which appeared to differ in the same set of factors. Intensive field work was carried out in the Waimakariri catchment (figure 6,1), but the performance of mature plants on other sites in the South Island (figure 0,1) was broadly compared.

A brief description of the Waimakariri sites follows.

Fig. 6,1.

Map showing the relative locations of the 4
populations studied in the Waimakariri catchment.

D.C. = Dry Creek

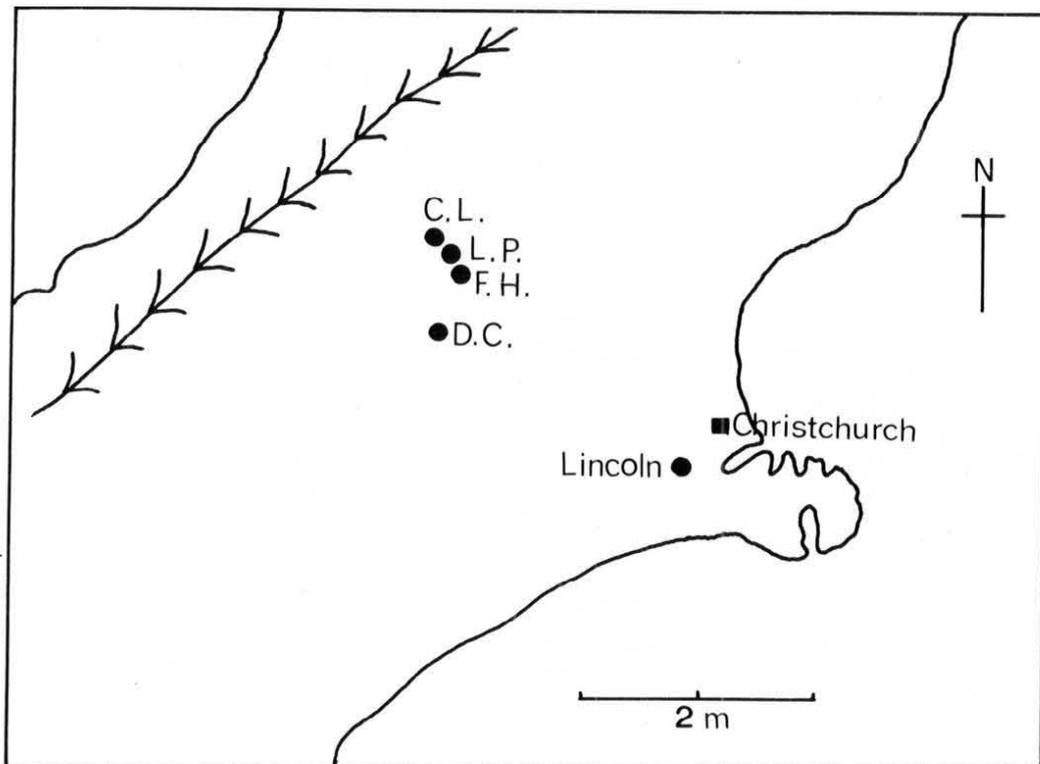
F.H. = Flock Hill

L.P. = Lake Pearson

C.L. = Cora Lynn

Fig. 6,2.

The alluvial site at Dry Creek.



Dry Creek (figure 6,2).

This site is on semi-stable margins of a gently sloping riverbed at 2,500 ft above sea-level. The surface consists of a series of uneven terraces and dry water channels of unsorted alluvium of greywacke sandstone. For most of the year the riverbed is dry, hence its name, but torrents of water pour down the valley after the spring thaw of snow off the surrounding peaks, and after high-intensity rains. This water cuts new channels and transports raw debris from upper to lower reaches. In general the riverbed is aggrading. Some lateral margins are more stable than others, supporting native and introduced forerunners of grassland, sweet brier, and other shrubs such as Discaria toumatou and Coprosma propinqua. Stable areas support dense grassland at the base of shrubs, and the topsoil is strongly melanised. Temperature inversions are strong, and frequent heavy frosts are experienced.

Sweet brier extends from this riverbed up the surrounding sunny slopes through an open short-tussock grassland community to c. 3,600 ft, where it finally gives way to subalpine snow-tussock grassland. At this altitude plants become stunted, making very little annual growth.

Flock Hill (figure 6,3).

This site is split into two contrasting habitats; the shaded or dark brier site, and the exposed or sunny brier site (441). They occur on opposite steep sides of the narrow valley through which flows the Craigieburn Stream. The dark brier site is on recently rejuvenated soils adjacent to existing beech forest (figure 3,1). These soils are stony and free draining yet seldom dry out. The fertility is higher than the podsolised soil under forest, and a lush carpet of Coriaria

Fig. 6,3.

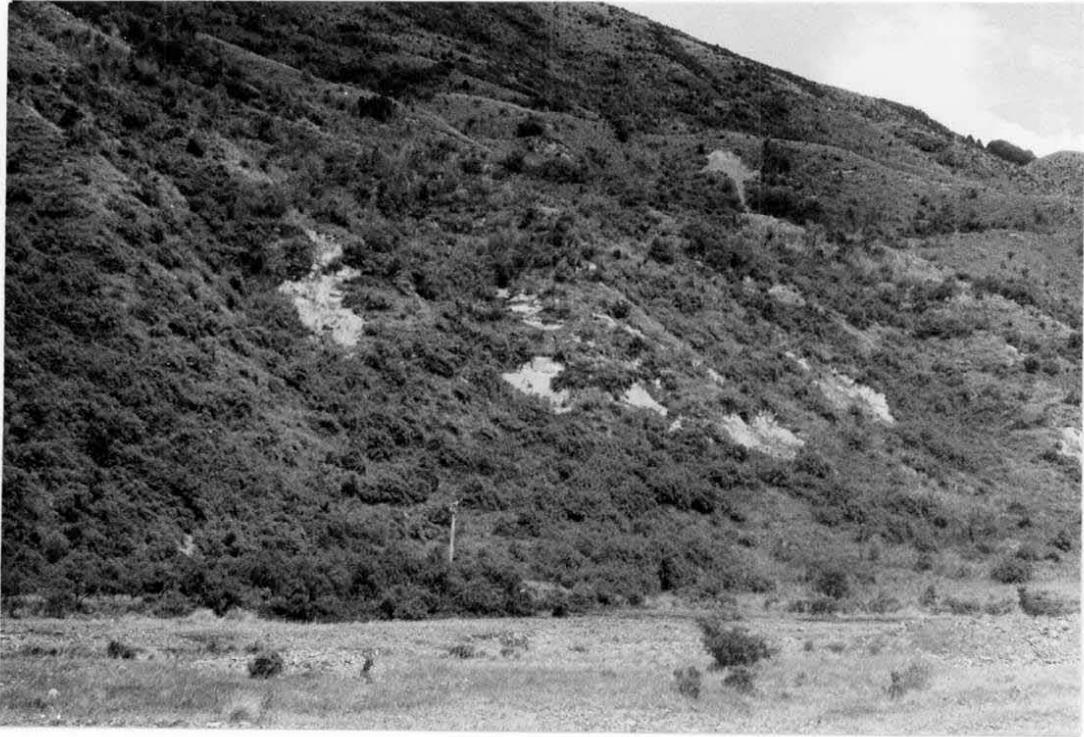
The sunny brier site at Flock Hill.

Note the evidence of soil slumping.

Fig. 6,4.

Part of the alluvial site at Lake Pearson, showing

the raingauge and thermometer in position.



sarmentosa and other herbs grows at the base of sweet brier and other shrubs.

The sunny brier site (figure 6,3) is on a slumped variant of a strongly leached yellow brown earth derived from greywacke drift and coal measure sandstones. Because of slumping, and lateral movement of drainage water through the profile, the "drift regime" has been activated and the soil is chemically more fertile than the adjacent stable soil under manuka. It has a tendency to dry out in the summer and is definitely drought prone. The altitude is 2,300 ft above sea-level.

Lake Pearson (figure 6,4)

This site is on an extensive alluvial fan which is probably of post-Glacial age, but has been periodically rejuvenated on the surface. The soil is an unclassified variant of recent soils and, like that of the previous sites, is stony and free draining, yet fertile. It supports dense scrub of sweet brier, Cassinia fulvida, Coprosma propinqua, and Discaria toumatou. The field layer consists of native and introduced herbs found in normal successions to short-tussock grassland. The aspect lies in a broad NE direction, and the altitude is 2,000 ft above sea-level.

Cora Lynn (figure 6,5).

This site occupies part of a large alluvial fan and part of the steep, actively eroding hillside nearby. Like the Dry Creek site, it combines a recent soil with a rejuvenated one, possessing the same features of free drainage and a high level of natural fertility. Sweet brier is the dominant shrub on the alluvial fan, but Discaria toumatou is a co-dominant on the hillside. The field layer is similar

Fig. 6,5.

General view of the alluvial fan and adjacent
hillslopes at Cora Lynn.



to other sites, representing successional stages to short-tussock grassland. This site lies well to the sun at an altitude of 1,800 ft - 2,300 feet above sea-level.

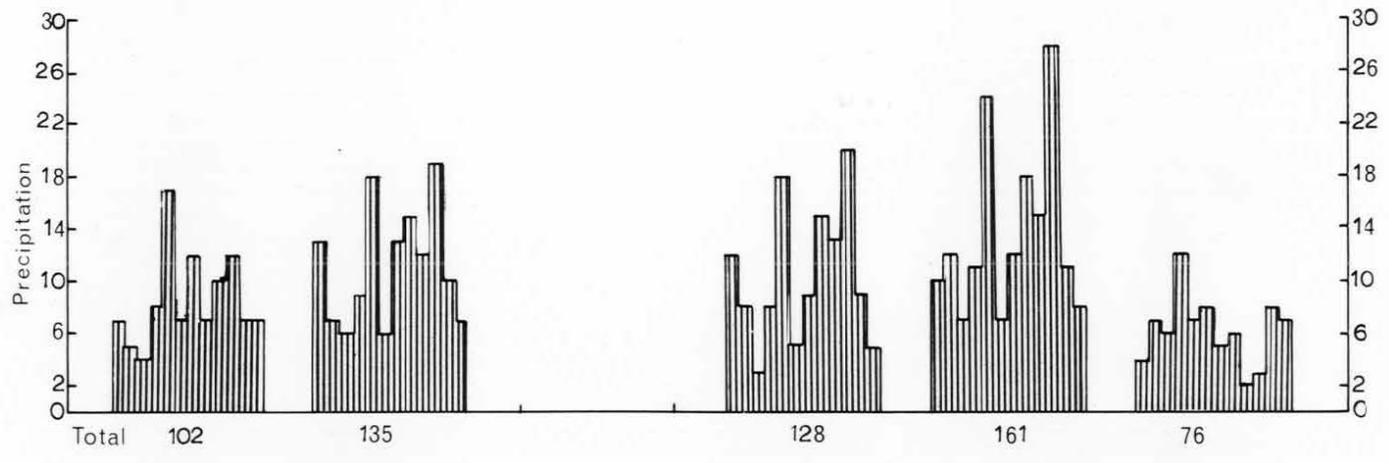
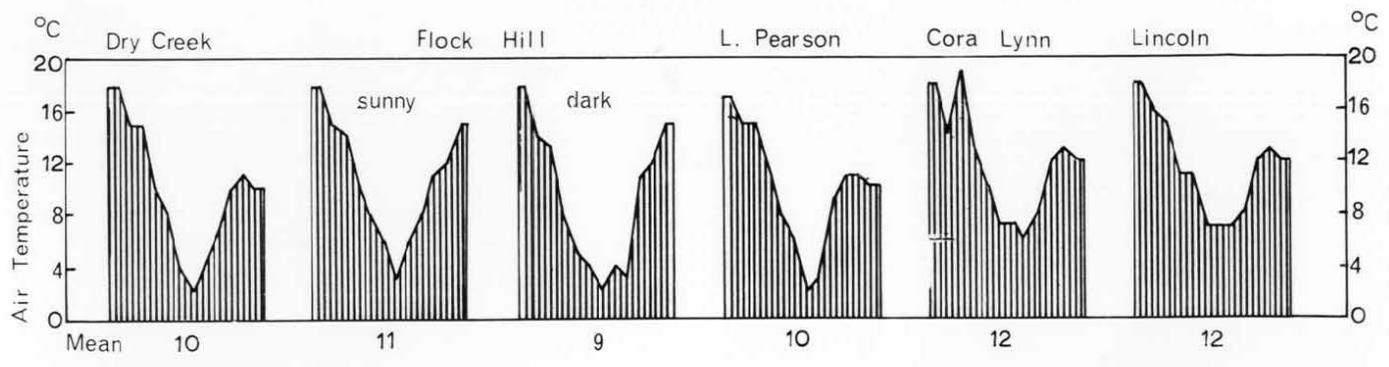
At each site a rangauge was installed in the conventional manner, and a Six's type maximum/minimum thermometer was set up 3ft above ground level and protected from direct insolation (figure 6,4). Frequent readings were taken from June 1961 to April 1963. The records from January 1962 to December 1962 are presented in Figure 6,6, together with rainfall and temperature data recorded at Lincoln College over the same period.

To summarise, the following features of these sites may be noted.

- (1) All are somewhat similar edaphically, namely free draining and fertile. The one exception is the sunny brier site at Flock Hill which is drought prone.
- (2) There is an increase in rainfall from Dry Creek to Cora Lynn.
- (3) There is a decrease in altitude from Dry Creek to Cora Lynn, accompanied by a general increase in mean temperature.
- (4) From the climatic viewpoint, Dry Creek is the poorest field site; Cora Lynn the best.
- (5) The high altitude site at Dry Creek is poorer for growth than the riverbed site, and at Flock Hill, the dark brier site is better for growth than the sunny brier site.
- (6) As will be demonstrated, plant growth follows an altitudinal gradient at Dry Creek, an aspect difference at Flock Hill, and a climatic gradient from Dry Creek to Cora Lynn.

Fig. 6,6.

Precipitation and air temperature recorded at
the 4 Waimakariri field sites, and at Lincoln,
Jan.-Dec. 1962.



SECTION 1. THE SHOOT SYSTEM611. Growth of stemsMature canes:

The first comparison concerns the diameter growth of mature canes. Measurements were made on healthy plants with approximately the same number of mature canes. As stated previously (452), the width of stems and annual rings varies with environment, the age of the cane, and distance from the apex (table 4,21). Sampling was confined, therefore, to the first 50 cm of stem from its base, since this section is fairly uniform in width. Measurements of basal diameters are presented in Table 6,1, which is divided into several sections indicating these comparisons

- (a) The climatic gradient from Dry Creek to Cora Lynn.
- (b) The altitudinal gradient at Dry Creek.
- (c) Aspect and light climate at Flock Hill.
- (d) Soil moisture on the sunny brier site at Flock Hill.
- (e) Grass competition at Dry Creek.

Table 6,1. Mean diameter (cm) of mature canes. n = 20 canes.

<u>Site</u>	<u>Habitat</u>	<u>Total width</u>	<u>Width wood</u>	<u>No. rings</u>	<u>Av. ring width</u>
(a)					
Dry Creek	Alluvium	1.88	0.46	6.3	0.073
Flock Hill	Colluvium	2.19	0.56	5.8	0.096
L. Pearson	Alluvium	2.01	0.57	5.6	0.101
Cora Lynn	Alluvium	3.31	0.84	7.9	0.106
(b)					
Dry Creek	2,500 ft	1.88	0.46	6.3	0.073
" "	3,600 ft	0.98	0.16	9.1	0.017
(c)					
Flock Hill	Forest	0.68	0.14	6.2	0.022
" "	Clearing	1.40	0.45	6.5	0.069
" "	Sunny	1.77	0.44	10.5	0.041
" "	Dark	2.19	0.56	5.8	0.096
(d)					
Flock Hill	Gley soil	1.26	0.27	7.9	0.034
" "	Convex slopes	1.30	0.32	10.9	0.029
" "	Concave slopes	1.77	0.44	10.5	0.041
(e)					
Dry Creek	Grassed				
	alluvium	1.57	0.37	10.9	0.033
" "	Raw				
	alluvium	1.88	0.46	6.3	0.073

These data confirm the expected pattern of plant growth as judged in the field from climatic records, soil examination, and differences in topography. They follow a similar pattern to that of seedlings, described in the previous chapter.

Perhaps the most substantial effects on the performance of mature canes observed in nature are those due to differences in soil moisture. Other things being equal, the closer soil moisture approaches a favourable level, the greater the response. This is demonstrated further in the following table, where the performance of canes in two contrasting habitats on a river floodplain under a 22" rainfall is shown.

Table 6,2. Mean diameter growth (cm) of mature canes at Rhoboro Downs. n = 20 canes.

Habitat -----	Total width -----	Width wood -----	No. rings -----	Av. ring width -----
Stony interfluve	1.39	0.30	10.3	0.029
Water channel	2.00	0.50	8.6	0.056

Basal shoots:

The differences in growth of mature canes between contrasting habitats is reflected in both the early growth of new basal shoots and their subsequent growth to maturity. The better site will favour much longer basal shoots with more nodes and longer internodes. The total width will be greater at comparable distances from the shoot apex, and there will be a wider pith and vascular cylinder, composed on the whole of larger cells, especially the vessels. The following table compares the poorest and best field sites in the Waimakariri catchment, and the differences in growth are attributed solely to contrasting macroclimates. Similar differences can be expected between habitats contrasting in light climate, soil fertility, soil moisture, and grass competition.

Table 6,3. Growth of new basal shoots (cm) at Dry Creek and Cora Lynn in 1962/63. n = 20 canes.

<u>Site</u>	<u>Average length</u>	<u>No. of nodes</u>	<u>Average length internodes</u>	<u>Total basal width</u>	<u>Width basal wood</u>
Dry Creek	240	82	2.92	1.20	0.30
Cora Lynn	325	100	3.25	1.80	0.50

Fruiting shoots:

The final comparison concerns the smaller shoots involved in flower and fruit production. A plant producing vigorous basal shoots and mature canes because of favourable supplies of external factors, might also be expected to produce vigorous fruiting laterals. That this actually happens can be demonstrated in practically any comparison which one may care to examine in the field, and this is illustrated here by the differences in fruiting laterals between the contrasting climates at Dry Creek and Cora Lynn.

In Table 6,4 two comparisons are drawn. First, the production of fruiting laterals borne in the canopy of mature canes, and second, the production of those borne on the previous season's new basal shoots. The latter are always more vigorous than the former, but the difference is proportionate to the growth conditions obtaining at the particular site.

Table 6,4. Length (cm) and fresh weight (gm) of fruiting shoots at Dry Creek and Cora Lynn in 1962-63. n = 30 shoots.

<u>Site</u>	<u>Shoot origin</u>	<u>Length peduncle</u>	<u>Weight peduncle</u>	<u>No. hips</u>	<u>Weight hips</u>
Dry Creek	Canopy	4.4	0.15	1.25	1.39
Cora Lynn	"	7.7	0.35	1.65	2.36
Dry Creek	Basal	11.9	1.12	5.20	7.01
Cora Lynn	"	23.7	2.87	8.40	12.52

612. Growth of leaves

Leaves of mature plants are as sensitive to changes in the physical environment as those of seedlings. Optimum physical conditions usually produce more and larger leaves, resulting in increased assimilation, greater root and shoot growth, and a larger food reserve. Small and/or chlorotic leaves are associated with a poor water balance, inadequate nutrients, harsh climate, or strong competition from other plants.

Symptoms of drought, inadequate nutrients, or plant competition are manifested by the yellowing of leaves in the canopy of mature canes, and premature leaf-fall (441). Leaves of plants growing in poorly drained sites become harsh and brittle soon after emergence from winter buds. Later on they become distinctly mottled, and develop lesions of the "black spot" fungus, Diplocarpon rosae. The net result is a reduction in assimilation and poor shoot and root growth.

The leaves, therefore, are important diagnostic organs, and are useful indicators of plant performance. But they vary considerably in size and number of leaflets according to their position, and the age of the shoot to which they are attached. Canopy leaves show less variation, and these were selected for study.

Measurements were made in the 4 Waimakariri populations during the 1962/63 growing season, and these will serve to demonstrate the effects of climate, mainly temperature and rainfall, on leaf growth. Within each population a number of leafy fruiting laterals were collected from the canopy of mature canes from as many plants as possible. From this collection, 100 shoots were selected at random and the largest leaf (usually the 3rd or 4th) was removed and its area was measured on an air-flow planimeter. After this, the leaves were oven-dried and weighed.

Leaf areas are shown in Figure 6,7, and leaf weights in Table 6,5. In both, the two forms of sweet brier (N type and A type) are compared. In addition, the data from the population of N type individuals at Omarama are included.

Table 6,5. Mean weight (gm) of leaves produced on mature canes in the Waimakariri catchment in 1961/62. n = 100 leaves.

<u>Site</u>	<u>Dry Creek</u>	<u>Flock Hill</u>	<u>L. Pearson</u>	<u>Cora Lynn</u>	<u>Omarama</u>
N type brier	.036	.038	.043	.048	0.018
A type brier	.025	.031	.038	.044	NA

NA = not analysed.

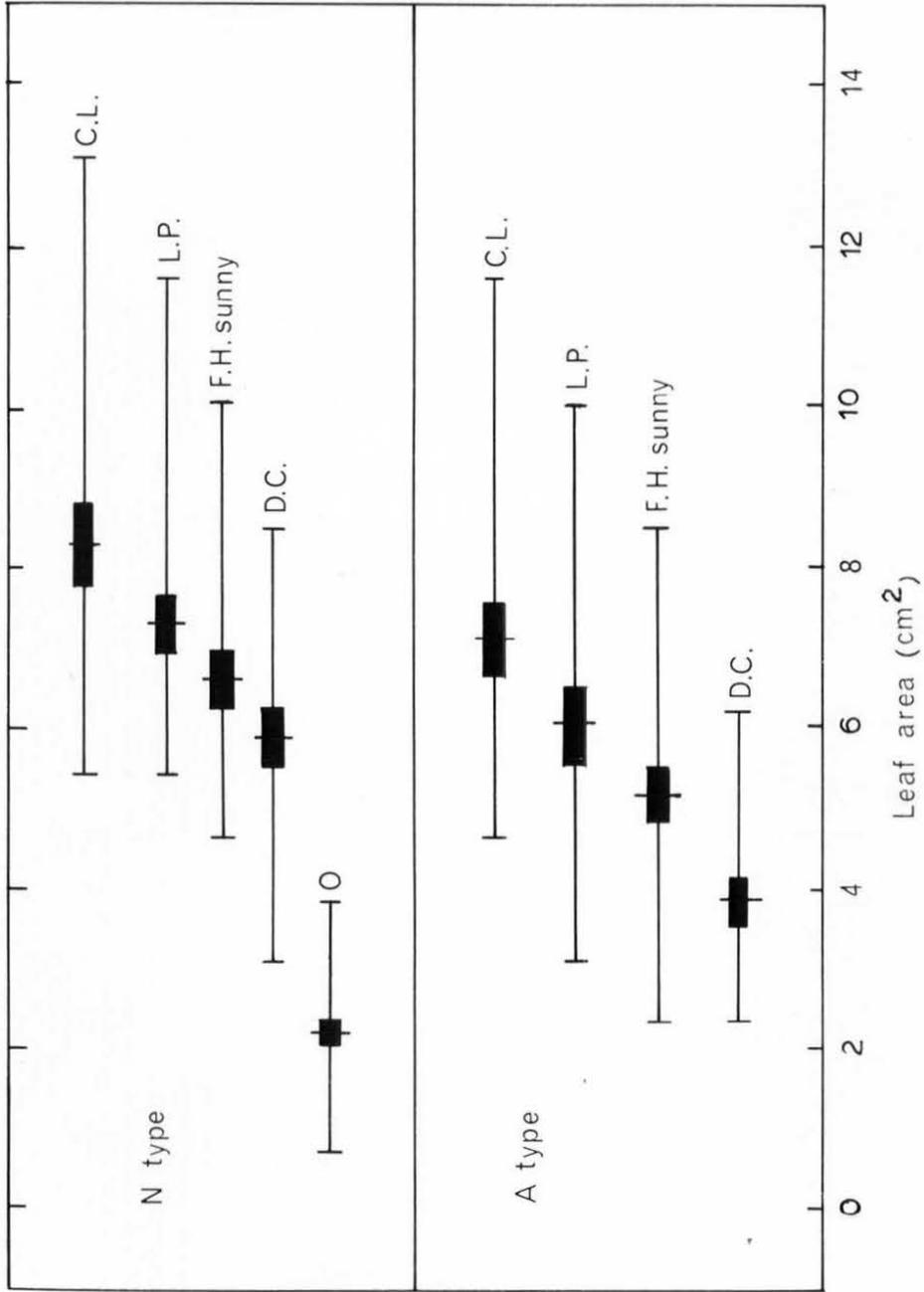
N type leaves were much larger than A type leaves at any one site, and within the two types of brier the differences between the means of adjacent populations were significant at the 5% level (Appendix 6,1). Leaf area and leaf weight increased in both forms from Dry Creek - the poorest field site, climatically - to Cora Lynn - the best field site. The leaves taken from plants growing on an excessively drained site under a 20" rainfall at Omarama were significantly smaller and lighter than anything produced in the Waimakariri catchment, except those produced at 3,600 ft at Dry Creek - the extreme limit of sweet brier. The area of these leaves averaged 2.7 cm^2 , with a mean oven-dry weight of .007 gm.

The same measurements were made during the 1963/64 growing season, and similar trends emerged.

200a

Fig. 6,7.

Relative changes in leaf area from Dry Creek to Cora Lynn in both N type and A type sweet brier. The range, mean, and standard error are given for each population sample collected during the 1961-62 season.



613. Discussion

The behaviour of mature plants throughout their range is analagous to that of seedlings and smaller plants. Plants will survive under a wide range of conditions, but will thrive only within a much smaller range. Sites in the latter category are those with the most favourable conditions of temperature, light, humidity, soil moisture, nutrients, and a minimum of competition and grazing. Such ideal conditions are found infrequently in nature and usually one or several factors limit growth.

In dry regions, as in Central Otago, the chief limiting factor for shoot and leaf growth seems to be soil moisture. If this is inadequate, plants are reduced in stature and vigour, with smaller stems and compressed annual rings. The leaves are small and pale yellowish green, and fall early. Flowering and seed production are also affected (632).

A similar response can be seen in plants growing at their extreme altitudinal limit or in competition with other plants for light, nutrients, and soil moisture. At 3,600 ft at Dry Creek, plants rarely exceed 2 ft in height and although the stems are markedly ring-porous, the outer rings are compressed, consisting of a single ring of vessels (early wood) surrounded by a narrow band of tracheids (late wood). Canopy shoots consist of a continuous series of bud scale scars, and the leaves they bear are small and chlorotic. Such plants are subject to insect attack and fungal infection and shoot mortality is high.

Shaded plants are tall and spindly with very few canes. The canes themselves are slender and sparsely branched, with long internodes and very few large and thin leaves. Annual ring widths are markedly compressed, showing that cambial growth is reduced.

Poorly drained soils and soils in which the water table periodically rises to or near the surface are inimical to the growth of mature plants, and produce features similar to those induced by drought or deep shade. Cambial growth is suppressed and leaves fall early. The canes are unhealthy and spindly, with many dead branches and short laterals.

Soil moisture is easily the most important factor affecting shoot and leaf growth within the climatic range of sweet brier. The water balance affects the functioning of leaves which in turn affect cambial growth and annual ring width. The rainfall in spring and summer is much more critical than that for the rest of the year, and the relationship between ring growth and rainfall shows that sweet brier is sensitive to variations in water supply during the growing season.

SECTION 2. THE ROOT SYSTEM

621.

It was shown (461) that the root system of sweet brier is made up of coarse roots, of which one or two are deeply descending and long-lived, and smaller roots and rootlets concentrated near the surface, which are short-lived. No measurements were made on the concentration or weight of roots at different depths because of the difficulties involved in sampling. The typical habitat is invariably stony, and coarse roots may penetrate to great depths, in an irregular fashion dependent on the ease of penetrability.

Naturally exposed profiles through coarse alluvium and colluvium show that root concentration decreases with increasing depth. The deeply descending coarse roots are as vigorous as the shallower ones,

but the abundance and branching of lateral roots decreases with increasing depth. The most common changes in soil conditions with increasing depth are: increasing soil moisture and nutrient supply, and decreasing aeration and penetrability. The latter explains the decrease in abundance and vigour of sweet brier roots with increasing depth.

The experiments discussed in Chapter 5 showed that increasing moisture and nutrient supply favoured root development in seedlings, but a high water table retards the development of a proper root crown, and suppresses fine roots. When the roots of mature plants growing in the gley soil at Flock Hill were examined, the coarse roots were weakly developed, possessing fine, sparsely branched laterals, and the root crown was weak. The poorest root system was observed within the forest habitat at Flock Hill. Here the coarse roots were confined to the deep layer of partly decomposed and undecomposed forest litter in a manner similar to that of most other understory shrubs. Only in forest clearings, where the litter layer is thin and soil movement has occurred, were roots seen to penetrate to greater depths.

The ability of coarse roots to penetrate to deeper levels is an advantage to plants subject to periodic drought or deep water tables, and those growing under strong competition from other plants, especially grasses. Under these conditions, the surface roots, which are mostly annual, decline in vigour and the plants become more dependent for survival on the deeper roots. That their overall growth is very much restricted is shown by the comparisons in shoot growth in Table 6,1. On the convex slopes at Flock Hill, the surface soil of greywacke drift

dries out rapidly in summer, and coarse roots grow down cracks and fissures in the underlying sandstone, with pockets of finer rootlets concentrated along the vertical rock faces.

On the well-grassed alluvium at Dry Creek, the surface roots of sweet brier compete strongly for nutrients and moisture with the dense mat of grass roots, but instead of descending to deeper levels, the coarse roots are concentrated near the surface, just below the grass roots. The reason for this is the constant high water table which prevents root development at deeper levels.

At Hakataramea, under an 22" rainfall, the sweet brier population is of exceptional vigour, contrasting with other populations receiving similar rainfall. An examination showed that most plants had deeply descending root systems which were able to draw on reserves of soil moisture from an unusually high water table caused by water flowing laterally through the profile from its source in the surrounding hill slopes.

In compact silt loams, and on strongly leached yellow-brown earths, the root system of sweet brier is poorly developed and shallow. In the first instance this is due to poor aeration and penetrability; in the second to a very low nutrient supply. This confirms the results found experimentally (Chapter 5). The most robust root systems with the best development of shallow roots were found on sites where coarse, stony soils had developed, but were well supplied with interstitial fine silts and clay. Evidently these sites have good aeration and penetrability, and are well drained. Also they are usually quite fertile.

SECTION 3. REPRODUCTIVE CAPACITY631. Vegetative extension

Unlike most of our native shrubs, sweet brier can produce new colonies of canes from underground shoots which emerge at some distance from the parent plant. Since they behave like roots in the early part of their development, they are dependent on similar soil conditions. The number and vigour of underground shoots is closely related to soil penetrability. Every plant has the potential to develop them, but unless the last requirement is satisfied, they do not as a rule appear.

The first indication of their presence is the emergence of a vigorous and highly pigmented shoot or sucker at some distance from the parent. This forms the basis of a new stool of canes which remains connected to the parent indefinitely (421 and 451). A single parent may produce two or more secondary colonies, which in turn may produce tertiary colonies, but the latter only occur in exceptional circumstances.

Compact silt loams and clays, poorly drained sites, and grass competition, retard vegetative extension. The best development is found on stony alluvium and colluvium, and on rejuvenated hill soils which are also usually stony. The young underground shoot emerges from the proximal region of the root crown and grows out laterally from the parent, just beneath the soil surface. Its vigour and direction of growth are determined by the nature of the soil. In very stony soils the shoot may be turned in several different directions with each annual increment before it finally emerges. One shoot examined finally emerged opposite its point of origin, having completely encircled the parent.

Dense colonies of secondary and tertiary stools are a familiar sight

on land previously infested with rabbits. The network of underground tunnels built by these rodents provides ideal conditions for development and long-distance extension of underground shoots. Many emerge from entrance or exit holes of old abandoned warrens.

Cutting or burning mature plants will also promote the development of new underground shoots and the emergence of older, dormant ones. In both cases a dense thicket of canes will arise, composed of natural regeneration from the parent stumps, and numerous suckers from underground shoots. Left undisturbed, most mature plants on favoured sites will produce one or two secondary colonies, but any increase in the density of the population is due mainly to an increase in the number of separate individuals.

632. Sexual reproduction

In section 1 of this chapter it was shown that there is a large variation in the potential capacity for shoot growth when sweet brier is growing under favourable conditions, and its capacity in various natural habitats. Since sweet brier fruits on current season's growth, its sexual reproductive capacity might be expected to show an equal amount of variation.

Adequate soil moisture and nutrients are required for maximum seed production of sweet brier throughout its range. Dry conditions during the growing season result not only in poor production of healthy fruiting wood, but a wide range of aspects concerned in sexual reproduction, such as poor flowering, abscission of buds, incomplete ovule development, and poor pollination and fertilisation. Even when the seed is set, dry soil

conditions may cause secondary degeneration of seeds, resulting in poor germination (Table 6,6).

Table 6,6. Percentage emergence of seedlings from seed produced in the Waimakariri catchment in 1960-61.
n = 400 fully-developed achenes.

Site -----	Habitat -----	Type of brier	
		<u>N</u>	<u>A</u>
Dry Creek	Alluvium	32.2	3.1
Flock Hill	Sunny	46.3	17.5
" "	Dark	64.0	-
L. Pearson	Alluvium	55.4	18.2
Cora Lynn	Alluvium	59.3	18.6

Note: percentages represent total emergence from 1961-64.
These tests were identical to those described in 414.

The 1960-61 season was poor for seed production, and phase droughts at Dry Creek and the sunny brier site at Flock Hill resulted in a high proportion of hip abortion and secondary seed degeneration, hence the low percentage emergence from seed produced at these sites. The contrasting high germination obtained from seed produced on the dark brier site at Flock Hill supports the contention that adequate moisture (and nutrients) during fruit formation is essential. This site is plentifully supplied with moisture at all times.

The overall effect of soil moisture on sexual reproduction can be followed in the Waimakariri catchment in a manner similar to that of shoot and leaf growth.

Within each population a large sample of "single" hips was collected from mature canes, and 100 hips withdrawn by the system of quartering. The volume of each hip was calculated by:

$$\frac{h}{6} (B_1 + B_2 + 4A)$$

where B_1 and B_2 are diameters of ends, A the median diameter, and h the height or length of the hip. After this, the hips were oven-dried and weighed. Hip volumes are shown in Figure 6,8, and oven-dry weights in Table 6,7.

Table 6,7. Mean weight (gm) of hips produced in the Waimakariri catchment in 1961-62. n = 100 hips.

Site -----	Habitat -----	Type of brier	
		N ---	A ---
Dry Creek	Alluvium	0.53	0.31
Flock Hill	Sunny	0.38	0.28
" "	Dark	0.62	-
L. Pearson	Alluvium	0.72	0.38
Cora Lynn	Alluvium	0.81	0.47

N type hips were larger and heavier than A type hips at any one site, and within each type there were significant differences between the means of adjacent populations (Appendix 6,2). Both hip volume and hip weight increased from Dry Creek to Cora Lynn along a previously described climatic gradient, with the exception of the sunny brier site at Flock Hill, where phase droughts during flowering and fruit set restricted fruit growth.

A further 100 hips of N type brier were selected from each population and these, together with samples from other habitats at Dry Creek, were subjected to other analyses (table 6,8).

Fig. 6,8.

Relative changes in hip volume from Dry Creek to Cora Lynn in both N type and A type sweet brier. The range, mean, and standard error are given for each population sample collection during the 1961-62 season.

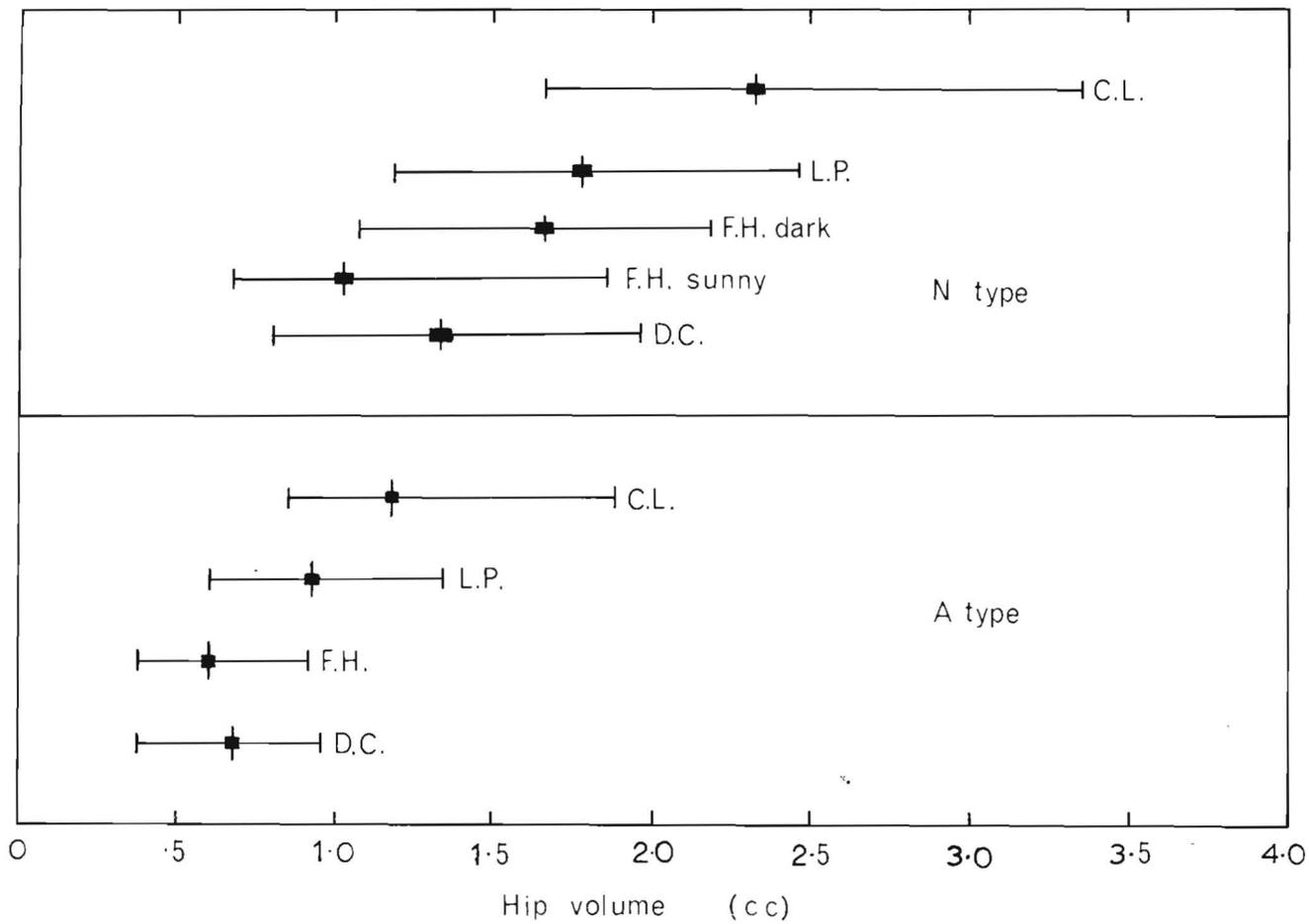


Table 6,8. Approximate reproductive capacity of sweet brier in the Waimakariri catchment for the 1961-62 season.
n = 100 hips and 400 fully-developed achenes.

<u>Site and habitat</u>	<u>Mean No.</u>	<u>Achenes Viability %</u>	<u>Weight (gm)</u>	<u>Output weight (gm)</u>	<u>Reproductive capacity</u>	<u>Reprod. weight (gm)</u>
Dry Creek						
2,500 ft	20.3	73	0.015	0.30	14.8	0.22
3,000 ft	23.1	94	0.014	0.32	21.7	0.30
3,600 ft	16.2	74	0.010	0.16	11.9	0.11
Flock Hill						
Sunny	10.9	56	0.014	0.15	6.1	0.08
dark	24.5	86	0.019	0.46	21.1	0.40
L. Pearson						
alluvium	23.1	80	0.016	0.37	18.5	0.30
Cora Lynn						
alluvium	25.3	85	0.018	0.45	21.5	0.39

Note: (1) Viability was determined by the tetrazolium test on 400 achenes, and oven-dry weights were obtained from further samples of 400 achenes.

(2) Reproductive capacity = product of mean number of achenes and fraction represented by % viability.

(3) Output weight = product of mean number and mean weight of achenes.

(4) Reproductive weight = product of reproductive capacity and mean weight of achenes.

(5) These data do not include an estimate of vegetative extension.

These results demonstrate the close relationship between hip volume and weight, and achene production, at the 4 sites (see figure 6,8 and

table 6,7). It appears that the potential reproductive capacity of sweet brier in this catchment follows the same gradients in habitat conditions to that of vegetative growth. With the exception of the drought-prone habitat at Flock Hill, there is an increase in number, weight, and viability of achenes, and thus reproductive capacity, from Dry Creek to Cora Lynn. The dark brier habitat at Flock Hill is equal in reproductive capacity to the best field site for vegetative growth (Cora Lynn), while the sunny brier habitat at this site is inferior to the high-altitude habitat at Dry Creek. At the last site the best habitat for reproduction is on the warm and well-drained yet well-watered mid-slopes at 3,000 ft.

Table 6,9. Approximate reproductive capacity of sweet brier in several South Island populations for the 1961-62 season.
n = 100 hips and 400 fully-developed achenes.

<u>Locality</u>	<u>Mean annual rainf. (in.)</u>	<u>Mean No.</u>	<u>Achenes Viability %</u>	<u>Weight (gm)</u>	<u>Reproductive capacity</u>
Hakataramea	22	23.4	73	0.012	17.1
Lindis Pass	19	22.4	75	0.015	16.8
Burkes Pass	27	20.3	83	0.010	16.8
Patearoa	15	17.5	67	0.010	11.7
Alexandra	13	16.3	69	0.009	11.2
Dusky	22	17.1	61	0.009	10.4
Cardrona Valley	24	9.4	55	0.013	5.2
Omarama	20	6.8	54	0.009	4.9
Rhoboro Downs	22	5.9	55	0.010	3.2

These results support the belief that available soil moisture during fruit formation is the chief environmental factor affecting seed production and potential reproductive capacity. In general, the higher the rainfall,

the greater the reproductive capacity. The three outstanding exceptions in the lower half of the table can be accounted for by below-average summer rainfall in this season, together with strong grass competition (Cardrona Valley) and excessively drained soils (Omarama, Rhoboro Downs). The effects of grass competition for available moisture were also apparent at Burkes Pass and Dusky. All these sites receive less rainfall than the Waimakariri catchment, and this is reflected by both the number and weight of achenes produced; the weights in general being much lower than in the Waimakariri catchment, and lower even than the average weight for the species (0.013 gm) reported by Salisbury (1942).

Although available soil moisture is undoubtedly important, available nutrients also influence fruit production (table 6,10).

Table 6,10. Comparative hip production on soils of different ages and nutrient availability at L. Pearson in 1961-62.
n = 100 hips.

Soil type	Relative age	pH	Organic P in total P %	Total N %	Organic C %	Weight hips (gm)
Bealey (1)	oldest	5.1	74	4.67	4.51	0.36
" (2)	interm.	6.0	44	3.70	2.80	0.42
Tasman	youngest	6.0	24	2.33	2.04	0.77

The Bealey (2) soil is an eroded variant of the Bealey (1), and all soils receive the same rainfall. Grass competition is strong on both Bealey soils and negligible on the Tasman soil, which is also much stonier and less mature. Although these factors must be considered, weights follow a distinct trend in phosphorus availability from the Bealey (1) soil to the Tasman soil.

Late spring frosts will also cause a severe reduction in reproductive capacity. In the 1962-63 season, a heavy frost during the first week of December resulted in severe abortion of hip primordia throughout the Waimakariri catchment and in other localities. Secondary seed degeneration was also high. The net result was a marked reduction in the number of fruits produced, low seed numbers and viability, and thus a low reproductive capacity.

633. Discussion

Sweet brier is sensitive to soil moisture during fruit formation, and effective moisture conditions must be present at this stage to stabilise the reproductive unit. Water availability affects fruit formation largely through its contribution to carbohydrate production. Dry soils restrict the uptake of nutrients, especially nitrogen and phosphorus, and growth is retarded. Adequate soil moisture ensures unrestricted growth of flower and hip primordia, and enhances pollination and fertilisation. Once the seed is set, continued high levels of soil moisture result in a greater weight of crop as individual fruits grow larger.

The effect of more favourable soil and climatic conditions is thus to increase hip and seed production, and raise the viability of sound seed. Thus the abundance of sweet brier on some sites can be attributed in part to the response of its seed output to favourable conditions, just as its relative subordination on other, drier sites can be partly related to lower seed output. There is an obvious tendency for high seed production to be associated with high rainfall

or effective soil moisture. There are indications that soil fertility may also be important in certain environments. A high level of available phosphorus may affect the reproductive capacity of sweet brier to a greater extent than vegetative growth, and thus play an important role in influencing the abundance and geographic distribution of the plant.

In most years sweet brier produces reasonable quantities of relatively large seeds which are effectively dispersed, and there is a strong chance that many will be deposited in suitable habits. The fate of the resulting seedling will depend in part on the weight of the seed, which is a rough approximation of the amount of food initially available. Once it is successfully established, the plant may extend into less favourable habitats by vegetative extension.

The reproductive capacity of sweet brier is an important factor determining its presence or absence in a particular environment, but it is not the only one. The number of seeds per unit area will depend also on the buried seed population, dispersal to and from the area, and the rate of destruction and decay of fallen seed. The establishment of the seedling is an even more critical phase in the life history of the plant (Chapter 7).

CHAPTER 7

THE ESTABLISHMENT OF SWEET BRIER

INTRODUCTION

This chapter is concerned primarily with the biotic effects on establishment of sweet brier. It is realised, however, that the division between biotic and physical factors is somewhat arbitrary. While it is easy to separate the effects of animals, phytophagous insects, and pathogens, plants competing with sweet brier exert their influence mainly by modifying the physical environment.

In the first part of this chapter, the biotic effects on seed and seedling survival are considered separately. Then the combined effects of all factors on seedling establishment are presented, and finally, all organisms associated with sweet brier are listed and discussed.

SECTION 1. AGENTS INFLUENCING SEED SURVIVAL711. Seed parasites

Before the seed of sweet brier falls to the ground or is dispersed by birds and animals, it is liable to attack from phytophagous parasites. Earlier (112 and 413), it was noted that the entire contents of seed may be destroyed by larvae of the rose seed chalcid, Megastigmus aculeatus. Sweet brier is a preferred host, but several other rose species (R. medwedewii, rugosa, alpinia, jundzillii, mollis) are also attacked (Milliron, 1949). I have observed it in Dog Rose seed as well.

The mature larva inhabits the achene in hips throughout the autumn, winter, and spring, undergoing diapause. Adults, which are predominantly female, synchronise their emergence with flowering of mature plants, burrowing through the achene wall and dry hip flesh, leaving a perfectly circular exit hole (figure 7,1). The females then oviposit either directly through the flesh of the young developing hip, or through the top of the calyx, depositing eggs within the immature achene where all the stages are passed to the adult. There is no external evidence of infestation, and by February the larva has consumed the entire contents and begins to pupate, emerging as an adult the following summer.

In a random sample up to 50% or more hips may be infested, but the number of achenes infested is far less since most are inaccessible. In Table 4,8 it was shown that out of a total of 200 achenes of N type and A type brier, 9.0% and 21.5% respectively were infested. The high percentage in A type brier is due to the reduced quantity of sound achenes which are available for infestation.

Milliron (1949) suggests that a truly random sample would certainly yield a lower percentage, not likely to exceed 10%, and probably within the range of 2-6%. Table 7,1 summarises the degree of infestation found in the 4 Waimakariri populations over 3 years. These counts were made in connection with viability and germination tests.

Fig. 7,1.

Adults of Megastigmus aculeatus.

Sound achenes on left, affected achenes with exit holes on right (x2).

Fig. 7,2.

Seedling emergence at Lincoln in 1962 from animal faeces collected in the field in 1961.

1. red deer - Dry Creek.
2. domestic cattle - Cora Lynn.

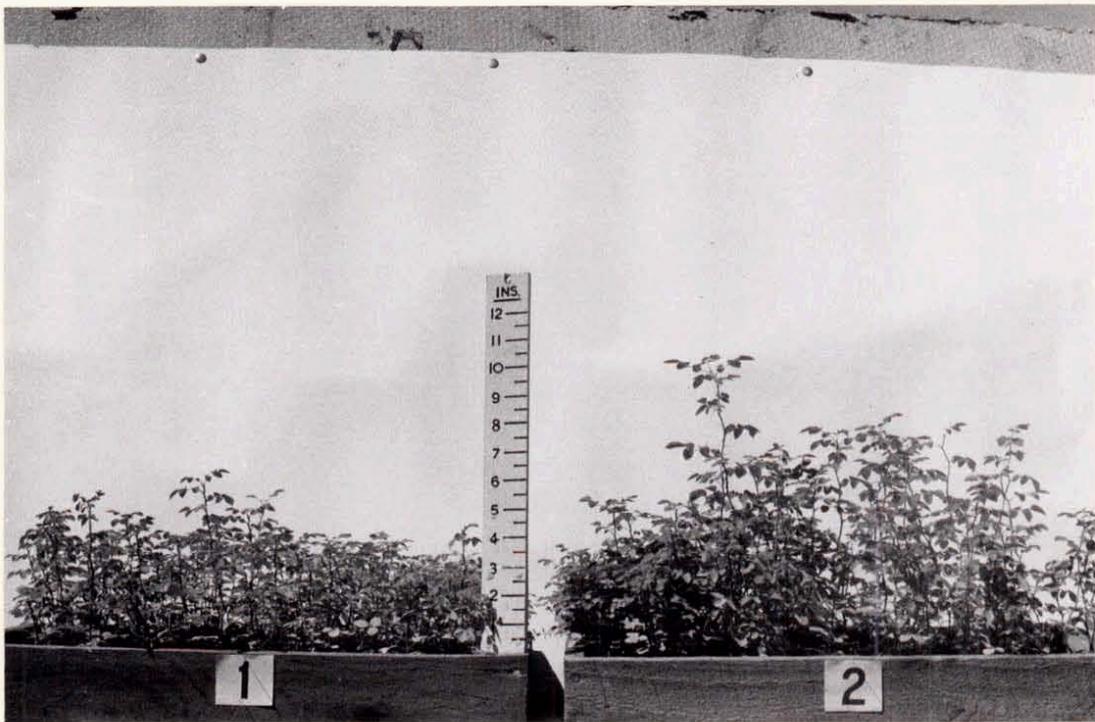


Table 7,1 - Percentage infestation of chalcid larvae in the Waimakariri catchment. n = 400 seeds.

Year	1959/60		1960/61		1961/62	
	N	A	N	A	N	A
Dry Creek	5.5	NA	18.7	21.3	18.5	19.0
Flock Hill	13.6	NA	1.0	20.7	19.5	20.0
L. Pearson	4.9	NA	16.2	8.0	9.5	21.5
Cora Lynn	18.2	NA	22.0	17.5	12.5	11.0

NA = not analysed

It appears that the degree of infestation is likely to exceed the expectations of Milliron, but is unlikely to retard the reproductive capacity of sweet brier. Further samples were analysed in 1961/62 from 10 other localities in the South Island. The mean degree of infestation was 12.0%, and the extreme range was 0.0% (Dusky) to 29.5% (Cardrona Valley). It seems that the degree of infestation depends on the density of the female insects, and suitable conditions for flowering and seed development. Low percentages were recorded in 1961/62 at high altitudes (0.5% at 3,600 ft, Dry Creek), in shaded habitats (1.2% at Flock Hill), and on very dry sites (0.0% at Burkes Pass).

No other seed parasites were observed.

712. Organisms involved in seed dispersal

The following animals and birds eat ripe hips and thus disperse seed of sweet brier: sheep, cattle, horses, deer, opossums, hares, rabbits, blackbirds, thrushes, and several finches (other birds may be included in this list but they were not observed in the act of eating). This evidence was derived either from field observations of eating habits or examination of faecal pellets. The grazing of hips usually takes place during winter when they are red and attractive, and other food is in short supply.

Sheep - these animals will graze freely all hips within their reach and disperse the seed in faecal pellets over wide areas. Favoured places for seed deposits are the numerous resting places on sunny slopes - flat terracettes. These sites are highly fertile from the accumulation of dung and urine, and veritable oases of high-fertility-demanding introduced plants. Many mature plants of sweet brier originate from seedlings which grow on the scarp face of these terracettes. Seed ingested by sheep is extensively damaged, but enough survive chewing to pass intact through the digestive system. Pellets dropped on open ground usually become hard, and seed will not germinate unless it is released into the soil and buried.

Cattle and horses - both these animals will graze hips freely and their browse line on plants is much higher than sheep. However, they are not as ubiquitous on pastoral land and their effect on dispersal is not as great. They also destroy a large quantity of seed by chewing, and drop their dung in a variety of sites. The dung usually becomes hard and unsuitable as a germination medium, but birds will often scratch among it and disperse sound seed to more suitable sites.

Deer - both red deer and chamois have been observed grazing hips, and will carry seed long distances, especially into forest edges and clearings. They also damage a large quantity of seed by chewing, but their faecal pellets seem to break down more readily than those of other animals, and sound seed is released into the soil.

Opossums - these animals are voracious feeders of hips and will scramble over plants in mid-winter and almost completely strip them of all fruit. For several weeks they seem to live on a pure diet of hips, and will disperse seed into forest, rock outcrops, and various types of scrub. They also destroy a large amount of seed by chewing, but their pellets break down easily, especially when living on a straight diet of hips.

Hares and rabbits - these animals are essentially herbivorous, but will eat hips within reach when snow lies on the ground covering their usual browse. The hare especially, will disperse seed over wide areas in grassland, but both destroy large amounts of seed, and their pellets become hard unless softened by rain or burial.

Birds - for several weeks during winter birds will live on a pure diet of sweet brier hips and the ground is literally covered with orange-coloured faecal pellets. Seed is taken in and passed unimpaired, and dispersed over wide areas. The pellets break down rapidly, often after overnight rain, and seed is washed into the soil. There is little doubt that birds provide the most rapid and effective means of seed dispersal, carrying seed to scrub and forest communities throughout.

Sound seed which passes through the animal digestive system will not

germinate the following spring, but in the second spring after ingestion, thus conforming to the normal behaviour of fallen seed (414). This was proved by marking and observing faecal pellets in the field, and by removing others to shallow flats at Lincoln (figures 7,2 and 7,3).

The viability of sound seed remains unaffected, likewise the number of seeds which actually germinate. In Table 7,2 the cumulative emergence of sound seed extracted from faecal pellets is presented.

Table 7,2. - Cumulative percentage emergence of sound seed extracted from faecal pellets. n = 400 seeds.

<u>Source</u>	<u>1961</u>	<u>1962</u>	<u>1963</u>	<u>1964</u>
Sheep	0.25	41.5	43.2	43.2
Cattle	-	14.7	44.2	45.0
Horses	0.25	24.7	30.5	30.5
Deer	0.50	34.2	44.2	44.2
Opossums	0.25	33.7	37.2	37.2
Rabbits	-	37.2	59.2	59.7
Blackbirds	-	32.0	39.2	39.2

Note: variation in final emergence is more likely due to seed provenance rather than the animal concerned.

713. Fate of fallen seed

Field observations were carried out to discover the fate of seed after it has fallen to the ground. It soon became apparent that field mice were destroying a large quantity of seed by dexterously splitting the achene along the line of suture, and scraping out the contents.

In a few instances the end of the achene had been gnawed off and the

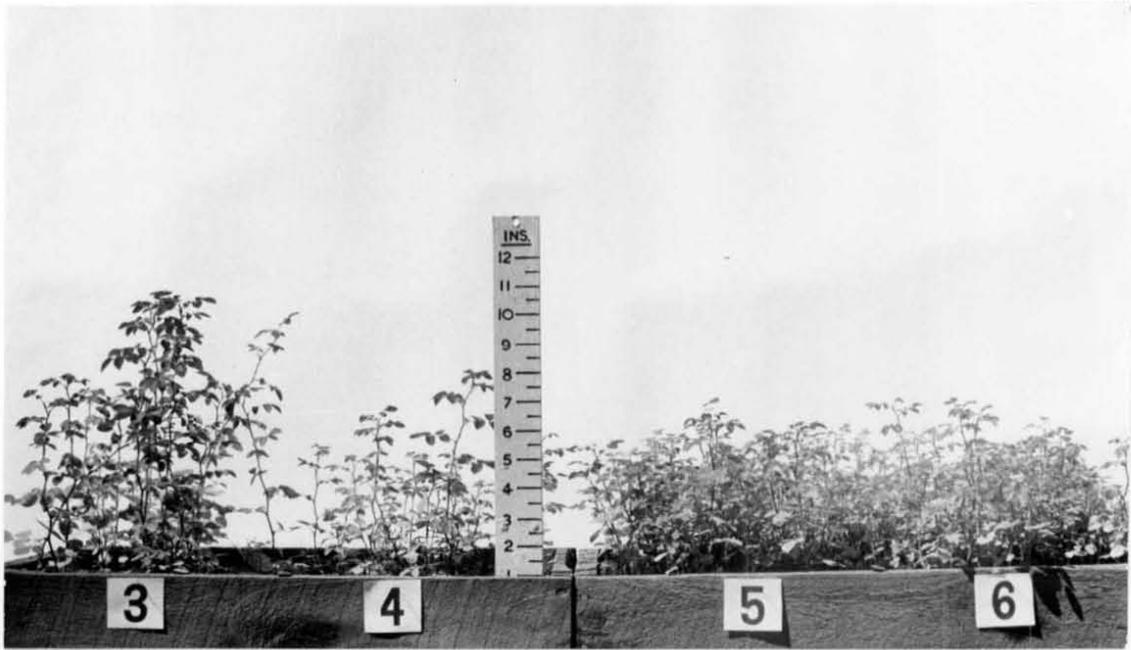
Fig. 7,3.

Seedling emergence at Lincoln in 1962 from bird and animal faeces collected in the field in 1961.

3. sheep - Dry Creek, 3,000 ft a.s.l.
4. rabbit - Lake Pearson.
5. blackbird - Dry Creek, 2,500 ft a.s.l.
6. opossum - Dry Creek, 2,500 ft a.s.l.

Fig. 7,4.

The snow-tussock grassland site at Porters Pass. Dense grassland dominated by Chionochloa rigida, with scattered shrubs of Dracophyllum acerosum.



contents withdrawn, but in most cases the achenes were split.

Mice are most active in winter and are found in almost every population of sweet brier. They seem to prefer the previous season's seed which falls to the ground periodically in dry, withered hips, and will even climb the plants in search of old seed, using the abandoned nests of various birds as food tables. By the end of winter, these nests are crammed with opened achenes and faecal pellets. Mice will also scavenge among litter and larger mammal faeces, removing achenes at will.

The seed-eating habit of mice was demonstrated quite forcibly on one rare occasion, when I noticed one of these small rodents making for its nest with a mouthful of old hips. The nest was crammed at one end with wrinkled hips - the winter food store. Because they seem to have so few predators in this country, mice play a significant role in destroying the seed of sweet brier. They operate in all habitats, except perhaps the very damp sites.

Although the achene of sweet brier is hard, it is liable to fungal attack as in the case of most fallen seed. I have no positive evidence to confirm this, but it seems to be the fate of seed which falls into deep litter, especially in beech forest, which is rich in fungi.

Despite these depradations, enough seed survives to germinate, as the abundance of seedlings each spring testifies.

721.

During 1961 and 1962 the history of numerous seedlings was followed by marking out permanent quadrats (1 dm²) in a variety of habitats, and plotting the position of seedlings each fortnight. The quadrats were laid down on 16 October 1961, and readings were terminated on 8 May 1962 (Table 7,3).

Table 7,3. - Mortality of sweet brier seedlings in their first year.

<u>Locality</u>	<u>No. of quadrats</u>	<u>No. at 16/10/61</u>	<u>No. at 7/11/61</u>	<u>No. at 7/2/62</u>	<u>No. at 8/5/62</u>
Dry Creek					
hillside	12	112	40	9	5 (4)
riverbed	28	167	93	47	37 (22)
Flock Hill	40	269	88	65	54 (20)
L. Pearson	25	167	115	80	21 (12)
Cora Lynn	22	172	109	45	4 (3)
Total	127	882	445	246	121 (14)

Note: the percentage of seedlings surviving at 8/5/62 is shown in brackets.

These results demonstrate that the supply of viable seeds is not limiting. The high mortality on the stony hill sites at Dry Creek and Cora Lynn make an interesting comparison with the better survival on alluvial sites at Dry Creek and Lake Pearson, and the slumped silty soil at Flock Hill. On average 50% of the seedlings appearing in October died during the next 3 weeks, and almost 75% failed to survive the first summer. Upon entering their first winter, only 14% remained.

Although mortality was high, probably very few seedlings died as a direct result of insect attack. Many disappeared altogether leaving no

remains. In a few cases where the seedlings were in damp shade, death resulted from damping-off. A few more had their cotyledons badly damaged by insects, and some were nipped off just below ground level. However, the majority of seedlings, except those which disappeared without trace, appeared to die from desiccation, especially those associated with other herbs. The effects of competition for nutrients, and of drought, were noticed frequently during the late spring and summer. The cotyledons and developing leaves quickly turned yellow, and the seedlings withered and died. In all cases, the seedlings were seen to make little growth, and their root systems remained superficial and sparse (cf. figures 4,7 and 4,27).

It was concluded that competing plants were the most powerful biotic factor affecting seedling survival in sweet brier. By comparison, the effects of insects and pathogens are insignificant.

SECTION 3. SEEDLING ESTABLISHMENT731. Experimental Methods

In 1961, broadcast-sown plots were laid down in the Waimakariri catchment to study more closely the factors involved in seedling establishment. Four metre square plots were pegged out in each of several sites representing different plant communities and habitats where sweet brier is present, and where it is absent.

Approximately 500 fully-developed achenes which were harvested from Dry Creek in 1960 were broadcast over each plot on 1 September 1961, using sawdust as a spreader. This gave a total of c. 2,000 achenes per site. In addition, a 6" furrow was made in the top left-hand corner of each plot, and 50 achenes from the same provenance were sown and covered with 1" of native soil. No artificial fertiliser was applied, and the vegetation was left intact. Any faecal pellets present were removed, and all plots were open to animal grazing and normal management. Although no achenes were visible on the ground before sowing, it is likely that some were present as a result of natural dispersal.

Soil samples from 0 - 4" were taken from outside the plots at each site, and placed in 4" porous clay pots after the larger stones and plant roots had been removed. Each site was represented by one pot. Fifty achenes from the same provenance were sown in each pot, and all pots were embedded in a sawdust mulch out of doors at Lincoln.

The behaviour of broadcast seed was closely observed at frequent intervals for the next two years. Likewise, the condition of newly-emerged seedlings.

A brief description of each field site follows.

- A. Snow-tussock grassland - Porters Pass (figure 7,4).
Altitude: 3,200 ft. Aspect: SSE. Slope: 18° .
% bare ground = 20. This site is just above the climatic limit of sweet brier. The vegetation consists of subalpine native herbs and small shrubs, and the soil is a strongly leached yellow-brown earth.
- B. Raw alluvial fan - Lake Lyndon. Altitude: 2,750 ft.
Aspect: WSW. Slope: 18° . % bare ground = 95. This surface is very young, a mixture of coarse angular rock debris set in a matrix of fine sands and gravels. The vegetation is sparse, consisting of indigenous colonisers and introduced perennial weeds.
- C. Rejuvenated hill soil - Dry Creek (Figure 7,5).
Altitude: 2,600 ft. Aspect: NNW. Slope 32° .
% bare ground = 50. This site is typical of modified and physically unstable sunny faces dominated by short-tussock grassland plants and introduced grasses and flatweeds. The soil surface is uneven, and terraced, with microsites of stable soil alternating with stone and soil pavement.
- D. Unstable river bed - Dry Creek (figure 7,6).
Altitude: 2,500 ft. Aspect: nil. Slope: 5° .
% bare ground = 60. This site differs from B in that there is more fine material and river silts in the matrix, and the vegetation succession is more advanced, many plants of the dominating short tussock are present.

Fig. 7,5.

The rejuvenated hill soil site at Dry Creek.
Note the surface stones, tussocks of Festuca novae-zelandiae, scattered grasses (sweet vernal) and young matagouri plants.

Fig. 7,6.

The unstable riverbed site at Dry Creek, showing the stony surface, tussocks of Festuca novae-zelandiae, and sparse inter-tussock vegetation.



- E. Stable riverbed - Dry Creek (figure 7,7). Altitude: 2,500 ft. Aspect: nil. Slope: 5° . % bare ground = nil. This site is situated next to D and differs from it by its more mature yet youthful soil, and its continuous inter-tussock cover of closely nibbled introduced grasses and native herbs.
- F. Unimproved short-tussock grassland - Broken River (figure 7,8). Altitude: 2,450 ft. Aspect: nil. Slope: 5° . % bare ground = 10. This site is located on an inter-montane glacial terrace which carried a humid form of short-tussock grassland with abundant browntop and sweet vernal. The soil is a strongly leached yellow-brown earth.
- G. Improved short-tussock grassland - Broken River. Similar to F in site details, but cocksfoot, white, red and alsike clovers have been over-drilled into the sward without destroying all the tussocks. Also, it has been topdressed with artificial fertiliser and the fertility has been raised.
- H. Improved pasture - Broken River (figure 7,9). Similar to F and G in site details, but the soil has been cultivated and the sward consists of ryegrass, cocksfoot, red, white and alsike clovers. Tussocks are absent. The natural fertility has been raised with artificial fertiliser.
- I. Beech forest - Flock Hill. Altitude: 2,400 ft. Aspect: SE. Slope: 35° . % bare ground = 5. This site lies just within the forest margin. There are very few shrubs, one native bramble and tendril climber, a few small beech seedlings, much moss, and c. 2-4" of leaf litter. The soil is a podsolised

Fig. 7,7.

The stable riverbed site at Dry Creek, showing tussocks of Poa caespitosa, and closely nibbled, dense grass in the intertussock spaces.

Fig. 7,8.

Unimproved short-tussock grassland at Broken River, dominated by Festuca novae-zelandiae, and the introduced sward grasses, browntop and sweet vernal.



yellow-brown earth.

J. Unimproved short-tussock grassland - Lake Pearson.

Altitude: 2,200 ft. Aspect: NE. Slope: 15°. % bare ground = 10. This site is similar to F in vegetative cover, but occupies a large alluvial fan. The soil is a strongly leached yellow-brown earth.

732. Results

Pot trial:

Table 7,4 summarises the germination of sweet brier in soil from the various sites. All seedlings emerged in the second spring following planting.

Table 7,4. Percentage emergence of seedlings in different soils.
n = 50 seeds.

<u>Site</u>	<u>Emergence</u>	<u>Site</u>	<u>Emergence</u>
A	84	F	90
B	90	G	86
C	94	H	86
D	74	I	88
E	72	J	82
		X	76

Note: X = potting loam

These results show that all soils were suitable as a substrate for germination, though seed in the field may differ markedly from that in disturbed soil samples away from their natural environment.

Broadcast Plots:

No germination occurred during the first spring and summer following sowing. Seedlings emerged in the following spring (1962) as expected.

Fig. 7,9.

Improved (cultivated) pasture at Broken River,
with ryegrass (Lolium perenne), white (Trifolium
repens), red (T. pratense), and alsike (T. hybridum)
clovers.



An abundance of seedlings appeared in the scarified rows of all plots except those on the forest floor at Flock Hill, where most of the seed had rotted, probably through excessive moisture and fungal attack. The success in all other plots demonstrated that seeds will germinate on a variety of sites providing they are effectively buried. The situation with broadcast seed was markedly different (Table 7,5). In the table, the sites are grouped according to similarities in habitat for germination and seedling survival.

Table 7,5. Emergence and mortality of seedlings in broadcast plots. n = c. 2,000 sown seeds.

<u>Site</u>	<u>Number at 30/10/62</u>	<u>Number at 18/1/63</u>	<u>Number at 26/4/63</u>	<u>Number at 18/10/63</u>
A	164	83	47	1 (11)
J	165	150	114	51 (19)
F	91	90	73	54 (21)
E	17	8	3	2 (7)
G	1	4	2	1 (7)
H	0	1	0	0 (2)
C	79	52	34	21 (39)
D	44	16	15	13 (6)
B	11	19	16	10 (2)
I	6	5	2	0 (2)

Note: number of new seedlings appearing enclosed in brackets.

Considering the large number of seeds sown, seedling emergence was very low; less than 10% being obtained in the best plots. The best emergence occurred in native tussock grassland communities with their abundance of litter and terrestrial bryophytes providing numerous vertical crevices the bottoms of which are moist and ideal microsites for

germination. Very few seedlings emerged from within the tussocks themselves. Seedling survival during the first year was surprisingly high, with the exception of the snowgrass plots where nearly all seedlings died either from insect attack in the summer, or from frost damage in the winter and spring. However, most of these grassland seedlings made very little growth because of strong competition from other plants for nutrients and soil moisture.

Germination and seedling survival was poor in closely nibbled grassland and improved tussock grassland, and poorest of all in improved pasture. Observations showed that much seed in these plots was suspended in the vegetation, and was destroyed either by extremes of temperature or mice damage.

Reasonable germination and survival were obtained on the unstable sites largely because the seeds were effectively buried. Poor germination but good survival was achieved on the raw alluvial fan. All surviving seedlings grew well in the absence of competition and in conditions of better fertility, reaching 3-4 times the size of seedlings in grassland. Poor results were obtained in forest plots for reasons already stated.

733. Discussion

The above results confirm an old forestry axiom that establishment is often difficult on the best sites, while poor sites give an abundance of poor seedlings. Sites which permit good germination are obviously not suitable later for establishment of seedlings. In the dispersal of sweet brier, both of these phases in its life history are critical. Both are influenced strongly by biotic effects, including land management, and the physical environment. Since these factors are more or less interdependent, it is unlikely that any one factor is controlling.

Compared with the seeds produced, there is a general absence of a spate of vigorous seedlings, particularly in scattered populations of mature plants. However, once the total area is increased, natural regeneration may become more reliable, but the number of seedlings which survive to maturity will be a function of the frequency of microsites which provide little or no competition, reasonable fertility, good drainage, and negligible grazing.

SECTION 4. ORGANISMS ASSOCIATED WITH SWEET BRIER741. Pathogens and phytophagous insects

The following is a list of pathogens and insects known to attack sweet brier in this country. Those marked with an asterisk have not previously been recorded.

Pathogens

Of the plant diseases identified from roses, the fungal pathogens are the important group found on sweet brier.

Phycomycetes

Phytophthora sp. Damping-off of seedlings.

Ascomycetes

Sphaerotheca pannosa (Walls.) Lev. Powdery mildew. Floccose mycelium smothers young seedlings growing under glass, shoot apices of plants in the field, and russeting of hips. A common primary pathogen causing stunting, and even death.

Leptosphaeria coniothyrium (Fuckel.) Sacc. Common stem canker. Secondary wood pathogen which can cause severe die-back in shoots.

Botryosphaeria dothidea (Fr.) Ces. and de Not. Brier scab. Secondary wood pathogen, often in association with the common stem canker, causing extensive shoot damage.

Griphosphaeria corticola (Fuckel.) Hohn. Secondary wood pathogen, occasionally associated with die-back. The conidial stage,

Coryneopsis microsticta (Berk and Br.) forms dark, disease lesions on hips.

Diplocarpon rosae Wolf. Black spot. Causes severe infection and premature defoliation of plants suffering from an excess of soil moisture.

Botrytus cinerea Grey mould. Found on hips in shaded and damp situations.

Basidiomycetes

Phragmidium mucronatum (Fr.) Schlecht. Rose rust. A primary pathogen causing severe malformation and cankers on shoots.

Insects

Hemiptera

Macrosiphum rosae (L.). Common rose aphid. Attacks young, developing shoots, causing minor damage.

Pentatrachopus tetraerhodus (Wlk.). Widely distributed aphid on sweet brier, its preferred host. Attacks developing flower shoots and basal replacement shoots, slowing down and retarding growth.

* Saissetia oleae Olive scale. Found on woody stems, particularly in drier districts.

Coleoptera

Pyronota festiva (Fabr.).

P. edwardsi Sharp. manuka beetles. Attack young shoots and foliage, and can cause severe defoliation.

Costelytra zealandica Brown beetle. Also attacks young foliage causing similar damage.

* Gastrosarus nigricollis Bates. Native long-horned beetle. The larva is stem boring, entering the canes of sweet brier by making a

spiral mine directed upwards through the vascular cylinder, thus destroying the stem above the mine.

- * Otiorhynchus sulcatus Black vine weevil. Larvae attack proximal region of roots causing death of canes and smaller plants.

Hymenoptera

- * Megastigmus aculeatus (Swederus). Rose seed chalcid. Larvae destroy the contents of achenes of sweet brier, its preferred host.

Arachnids

Acari

- * Tetranychus telarius (L.). Red spider mite. Found on stems and particularly leaves in dry climates, causing decolouration and debility.

Sweet brier attracts numerous other insect visitors, particularly during the flowering season. The flowers themselves are always infested with thrips, but as far as I could detect, they cause no visible damage.

742. Browsing animals

Rabbits, hares, and larger mammals will browse mature plants of sweet brier, especially the soft new shoots and ripe hips. Once the shoots develop secondary wood, and the prickles harden, they are neglected.

The effects of animal grazing are particularly noticeable among seedling populations. The pressure which the rabbit exerted on seedlings and juvenile plants is well enough known, and since the number of rabbits has diminished considerably, the increased density of sweet brier is often associated with lax or infrequent grazing. Where sheep numbers have been

kept high, the spread of sweet brier since the rabbits were destroyed has been very limited, because of the close grazing of these animals. Where the management has changed from sheep to cattle grazing, as in parts of Marlborough province, the spread of sweet brier has been enhanced.

Infrequent or lax grazing allows sweet brier to enter neglected grassland in drier areas, as is evidenced by the outstanding fence-line contrasts and zonation of scrub within and between individual farms or properties.

743. Beneficial organisms

According to Maeda (1954), endotrophic mycorrhiza occur in the roots of several members of the Rosaceae, including Rosa polyantha. Examination of sweet brier roots from this viewpoint yielded negative results. Some blue-green algae were found attached to, and penetrating into, the lateral rootlets of seedlings growing on the forest margin at Flock Hill, but I did not attempt to identify the algae concerned.

Morrison (1961) has shown experimentally that the nodules of the native matagouri shrub (Discaria toumatou) are capable of fixing atmospheric nitrogen. He suggests that these nodules may be able to support the growth of matagouri in nature, and perhaps even that of its usual associates such as sweet brier. Although this may be true where the two species coexist, it does not explain the source of nitrogen of the numerous individuals and populations of sweet brier growing in the absence of matagouri.

Several insects pollinate the flowers of sweet brier. Among the most important are the bumble bee (Bombus terrestris), hive bee (Apis mellifera), a hover fly (Syrphus novae-zealandiae), and the small native bee. The latter is especially active, and pollen examined from trapped specimens belonged entirely to sweet brier.

Several, unidentified hymenopterous larvae predate on casual visitors to sweet brier flowers and hips, and the larvae of the hover fly predate on both species of aphid found on sweet brier.

CHAPTER 8

CONCLUDING DISCUSSION

It is generally held that introduced plants are inferior to the natural vegetation of an area when it comes to a struggle for existence. This argument is strengthened by several examples in the wetter parts of New Zealand where introduced weeds such as gorse and broom have ultimately been replaced or are being replaced by native plants which are assumed to be better adapted to New Zealand conditions. Some native plants such as bracken (Pteridium aquilinum var. esculentum) and manuka (Leptospermum scoparium) are so aggressive in certain areas, especially after fire, that they also can acquire the mantle of unwanted plants or weeds.

However, the argument is considerably weakened when applied to the drier regions of the eastern South Island. In these regions the native vegetation itself is ecologically impoverished and poorly adapted. Thus it is easily destroyed and difficult to re-establish. Soils, climate, and topography are extremely diverse, yet distinctive enough and in contrast to other parts of the country. The activities of man, both Polynesian and European, have encouraged certain types of vegetation at the expense of others, and created a number of new habitats, especially those of bared ground. For reasons of their poor adaptability to both the old and new ecosystem, native plants are slow or fail to exploit these habitats fully. In the absence of predators or disease, and with weak competition, a variety of introduced plants find these conditions suitable for dispersal and establishment, and thus rapidly

increase in abundance and distribution.

Sweet brier seems well suited to this situation, as it is essentially a plant of open habitats, colonising bare ground at an early stage. Also, it is quite able to compete with sparse vegetation, and is a true opportunist.

There are several outstanding features of sweet brier which contribute to its adaptability and success:

- (1) It tolerates a wide range of environment, extending throughout the country in various habitats from dry rock outcrops to clearings within forest. But it thrives within a much narrower spectrum which embraces a large part of the South Island short-tussock grassland environment.
- (2) Its structure, life history, and seasonal behaviour are well suited to the long, cold winters and a comparatively short yet active growing season which are experienced in the above environment.
- (3) Its capacity for partial or complete self-fertilisation ensures a satisfactory seed set in most of its habitats and, since a large number of hips may be formed each year, a high seed output and reproductive capacity results. Thus dispersed infestations can thicken up very quickly given suitable conditions for seedling establishment.
- (4) The colourful, succulent hips provide an attractive food source during winter for fruit-eating birds and most animals, and a large number of seeds is rapidly and effectively dispersed in this manner.

- (5) The seeds possess a variable dormancy, and although total germination is rather low in comparison with some plants (rarely more than 50% is achieved), seedlings will appear for at least four years from the same seed lot. This inherent feature reduces the risk of total loss if germination is followed by poor conditions for seedling establishment.
- (6) Underground shoots from which stem suckers arise provide an efficient means of vegetative extension and the development of new though not independent colonies of shoots. Few native shrubs have this facility.
- (7) Mature plants are capable of providing new shoots rapidly and repeatedly after cutting or burning, and when mixed thorny scrub is treated in this manner it is converted to a pure sweet brier thicket within 3-5 years.
- (8) Root growth of seedlings is rapid and the root system of mature plants is extensive, tolerating a wide range of soil conditions.
- (9) The heavy armature of stout, hooked prickles mixed with short aciculi enable the plant to attain maturity and maintain itself in the face of animal grazing. Only in its younger, more succulent stages are the shoots susceptible to grazing damage, but at this stage there is usually an ample amount of alternate forage.
- (10) The species can be regarded as a polyploid, permanent hybrid and, as with other plants of hybrid origin, its extraordinary aggressiveness in colonising disturbed habitats may be

attributed to the permanent possession of hybrid vigour and a favourable combination of genes.

Few native plants possess all these attributes. Matagouri (Discaria toumatou) alone resembles sweet brier, and in several respects the two species are almost identical. The strongest competitors of sweet brier in the short-tussock grassland environment appear to be not native plants, but other introduced plants, usually of a different growth form.

The field and experimental evidence proves that seedling establishment is the most critical phase in the life-history of sweet brier. Seedling mortality is high, and there is a negative correlation between seedling growth and the density and vigour of competing grasses. The most significant fact which emerges is that sweet brier seedlings are clearly vulnerable to conventional pasture improvement, thus confirming the observation that a well managed pasture is generally hostile to establishment of nearly all woody plants.

There is little doubt that sweet brier briefly exploited the ecological vacuum in the short-tussock environment created by wholesale destruction of rabbits, perhaps the most effective biological agent retarding its increase in abundance. But the evidence suggests that after 10 - 15 years it is rapidly approaching its zenith in abundance, though it will continue to spread, but in a more discontinuous fashion. Many populations show an apparent increase in density, but this can be attributed to the growth of established plants, most of which are very small and of great age (\pm 10 years), pre-dating the spectacular increase in natural revegetation. Many of these mature plants are declining in

vigour because of increasing competition from herbaceous vegetation. There is a distinct regeneration gap in most populations that I have examined, with a paucity of second-year and older seedlings. Those that are present are weak-stemmed and monaxial, and mortality is high in the face of strong grass competition. Nevertheless, in the space of 100 years, sweet brier has become firmly established in a variety of habitats beyond the physical and economic limits of pasture improvement, and failing its total elimination by biological or other control agents, it will remain as a prominent member of the introduced flora of New Zealand.

SUMMARY

A study of the factors involved in the establishment of sweet brier in New Zealand is described. In order to provide the necessary background, the identity, structure, life history, and seasonal behaviour of the species are discussed in some detail.

Two forms of sweet brier can be recognised; one is a normal, fertile form conforming with published descriptions of the species; the other is a male-sterile, aberrant form which is more vigorous in vegetative growth, but less abundant. Both are sexual and self-fertile, but not exclusively self-pollinated. There are no apparent differences in ecology.

Flower primordia are initiated on the new season's growth, the first flowers appearing in October-November. Usually one crop is produced each season, but a light second crop in February-March is not infrequent. As a rule plants will flower in their third season under glass, but in nature flowering begins much later.

The seed is exalbuminous, consisting of two cotyledons and an embryo. It ceases to grow by mid-February and may remain within attached hips for several years. An average plant will produce c. 500 hips in a season, each containing 15-25 full-developed achenes. The potential germinative capacity of ripe seed - as determined by the tetrazolium staining method - is high, often exceeding 80%. Seedlings will appear in the field during a limited period each spring. Germination of individual seed lots is erratic, extending over at least 4 years, and peak germination occurs in the second spring following seed production. It appears that this variable dormancy is caused by the mechanical

restriction imposed by the pericarp, and growth and germination inhibitors contained in the achene.

Degeneration of seed in artificial storage is very slow, but under natural conditions both the potential germinative capacity (viability) and seedling emergence may be seriously retarded, especially if the seed is ineffectively buried, buried too deeply, or lodged in damp soil.

The mature plant consists of a long-lived crown from which arise woody, perennial shoots. Shoot growth is determinate, and branching is definite or cymose. New shoots arise annually, thus enlarging the colony and replacing old or injured ones. Young shoots are at first succulent and pigmented, but later they become lignified and thorny. Veteran plants are difficult to age because of their multiaxial growth habit, though individual shoots 15-20 years old are not uncommon.

The first leaf of seedlings is unifoliate, but successive leaves are more complex, attaining 7-9 leaflets. Most of the leaves are shed between March and May, and at abscission they are usually pale green, except in droughty soils, when they turn yellow, and fall early.

Vegetative buds of seedlings and juvenile plants open first in August, followed by the fruit buds of adult plants. When young flower buds become visible, basal crown buds swell, giving rise to vigorous replacement shoots. Apical dominance is pronounced in adult shoots, but is less closely observed in seedlings and juvenile plants. Winter buds can be induced to grow at any time by exposure to high temperatures regardless of daylength, and without winter chilling.

The duration of growth in fruiting shoots is determined largely by the number of initials already laid down in resting buds. Vegetative

buds unfold more leaves than were present in resting buds, and may continue extension growth into April. Growth in diameter is apparently dependent upon active extension growth. Cambial activity begins simultaneously throughout the shoot and is dependent upon the presence of expanding buds. When extension growth ceases, cambial activity also ceases.

The root system of mature plants is extensive, consisting of radiating, coarse roots, fine lateral roots emanating from coarse roots, and fine rootlets, mostly annual, concentrated near the soil surface. Underground shoots which root at the nodes may also be regarded as functional roots. Root growth begins before the aerial buds open, and continues long after aerial shoots cease extension growth.

Parasites and predators reduce the quantity of sweet brier seeds which eventually germinate. The larvae of Megastigmus aculeatus kill seeds while they are still on the plant, and mice will eat both attached and fallen seed. Other animals will also destroy large numbers of seeds. When the seed finally falls, germination will not take place for at least 12 months. During this period many seeds rot. Despite these factors, seedlings appear in relative abundance in most years, because of the high reproductive capacity of most plants.

Although mature plants with their extensive root systems can withstand drought conditions and grass competition, seedlings are less tolerant and mortality is high. The influence of light climate, soil conditions, and plant competition on seedling growth was studied and it was found that low light intensity, high water tables, and compact soils reduce both top and root growth. Competition for nutrients and

soil moisture is very important in the establishment of sweet brier. The reduction in growth of seedlings in the presence of grass is spectacular, and grasses stimulated by added fertiliser provide the strongest competition. During the initial growing season, competition may stunt or kill the seedling. However, in more open grassland competition may not prevent successful establishment in wetter seasons. Even so, a reduction in competition would accelerate invasion. Thus the establishment of the individual plant is the most critical phase of its ecesis.

Once the plant is established it begins to dominate the area around it. The extent of this domination depends on the favourability of the site and the level of land utilisation. Fire usually results in a marked increase in its dominance at the expense of other species. The altitudinal limits of sweet brier are set by climatic conditions, but within its climatic range soil conditions, especially the availability of phosphorus, are very important, as also is the open nature of many of its natural habitats.

It appears that much of what is called current sweet brier invasion of pasture land represents the growth to maturity of subdued seedlings many of which pre-date natural revegetation since the rabbit was eliminated. Seedlings invaded these areas in the past because they were maintained in an open condition. They continue to maintain themselves on these areas but do not appear to be invading the surrounding grassland.

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APPENDIX2,1. Technique for determining pollen viability.

- (1) Gather flower buds as they are about to open and place in envelope; leave in warm, dry place to dry.
- (2) Pull off corollas and shake pollen on to a clean slide.
- (3) Add one or two drops of 30% alcohol to disperse grains, but do not allow the slide to dry out completely.
- (4) Place a small amount of Owczorzak's jelly dye on to slide and heat gently, allowing the liquid to flow freely over the grains.
- (5) Place on a cover slip so that the dye reaches its outside edges.
- (6) Allow to cool, and store for later examination.
- (7) Count 500 grains under low power (x100), and calculate % of functional pollen.

In sweet brier, the functional grains expand and the cytoplasm is stained red (phloxine). Non-functional grains remain shrivelled and blue-green (methyl green).

4,1. Topographical tetrazolium staining method for determining seed viability.

- (1) Soak 400 achenes in water for 18-20 hours.
- (2) Cut off a third of the achene at the broad end opposite the radicle.

- (3) Immerse the cut radicle parts of the achenes in 1% tetrazolium solution (chloride or bromide) for 24-48 hours at 30° in the dark.
- (4) Extract the embryo from the achene.
- (5) The following seeds are considered viable:
- a. completely stained embryo (figure 4,3 a).
 - b. embryo showing an unstained point at the radicle tip.
 - c. embryo showing unstained spots at the cotyledon opposite the radicle, allowing superficial necrosis up to half of the cotyledon, and a pervading necrosis up to one-third of the cotyledon (figure 4,3 b).
 - d. cases b and c combined.

This technique is adopted by the International Seed Testing Station Rules.

5.1. Interaction table for Table 5,18.

Interactions significant to 5%
Weight (gm) of roots 0-8 cm

P x N

Treatments	No N	N
No P	1.155	0.522
P	2.325	6.038

- 5.2. List of plant species and their frequency, growing in native Tekapo soil used in competition experiment. a = abundant; f = frequent; o = occasional; r = rare. * = introduced species.

Aciphylla aurea r	Geranium sessiliflorum o
Agropyron scabrum o	Gnaphalium collinum o
* Agrostis tenuis a	* Hieracium praealtum f
* Aira caryophyllea f	Hydrocotyle novae-zelandiae o
* Anthoxanthum adoratum f	* Hypochaeris radicata f
Brachycome sinclairii f	Leptospermum scoparium r
Carex wakatipu f	* Linum catharticum f
Carmichaelia monroi o	Luzula campestris o
Celmisia gracilentata f	Oreomyrrhis rigida o
* Cerastium vulgatum o	Pimelea pseudo-lyallii f
Coprosma petriei f	Plantago spathulata o
Cotula perpusilla o	Poa colensoi f
Craspedia uniflora r	Pyrrhanthera exigua o
Cyathodes colensoi f	Ranunculus lappaceous o
C. fraseri a	Raoulia subsericea f
Deyeuxia avenoides o	* Rumex acetosella f
D. forsteri f	Scleranthus uniflorus o
Discaria toumatou f	Senecio bellidioides f
Epilobium elegans o	Stackhousia minima o
Euphrasia zelandica o	Viola cunninghamii f
Festuca novae-zelandiae a	Wahlenbergia albomarginata f
Gaultheria depressa o	
Gentiana serotina f	

5.3. Indices for quick tests given in Table 5,19.

Ca : parts per 40,000 of extract, using soil solution ratio of 1:5 (extractant solution: normal ammonium acetate).

K : parts per 250,000 of extract, using soil solution ratio of 1:5 (extractant solution as above).

P : parts per 50,000,000 of extract, using soil solution ratio of 1:200 (extractant solution: 0.002 normal truog reagent buffered with ammonium sulphate to pH 3).

5,4. Interaction tables for Table 5,20.

Yield (gm) of grass and grass plus clover tops

<u>P x N</u>	1st harvest 1%			3rd harvest 5%		
	Treatments	No N	N	Treatments	No N	N
No P	0.61	0.88		No P	6.76	9.18
P	3.09	26.74		P	8.65	5.86

<u>S x moisture</u>	1st harvest 5%		2nd harvest 5%		3rd harvest (just below 5%)	
	Treatments	No S	S	No S	S	No S
Dry	7.62	8.56	6.84	7.86	5.25	6.29
Moist	7.95	7.18	7.99	5.98	10.80	8.11

<u>P x S</u>	2nd harvest 1%		
	Treatments	No S	S
No P	4.05	5.36	
P	10.78	8.48	

<u>S x grass</u>	2nd harvest 5%		
	Treatments	No S	S
Cut grass	6.69	7.54	
Cut grass + clover	8.14	6.30	

N x moisture 3rd harvest 5%

Treatments	No N	N
Dry	7.00	4.54
Moist	8.41	10.50

5,5. Interaction tables for Table 5,21.

Total yield (gm) of grass and grass plus clover tops
Interactions significant to 1%

P x N

Treatments	No N	N
No P	23.1	25.7
P	32.9	69.5

P x grass

Treatments	Cut grass and cut grass + clover	Uncut grass
No P	22.06 bB	29.00 bB
P	38.56 aA	76.50 aA

Moisture x grass

Treatments	Cut grass and cut grass + clover	Uncut grass
Dry	27.31 a	39.50 bB
Moist	33.31 a	66.00 aA

In the last 2 interactions, the Duncan letters refer to the differences P and moisture make, i.e., they are to be read down only.

S x N Weight (gm) of roots 12-20 cm

Treatments	No S	S
No N	0.95	0.67
N	0.77	1.54

5,6. Interaction tables for Table 5,22.

Yield (gm) of sweet brier roots 0-8 cm

Interactions significant to 5%

P x S

Treatments	No S	S
No P	0.139	0.198
P	0.198	0.109

N x moisture

Treatments	No N	N
Dry	0.192	0.079
Moist	0.145	0.229

5,7. Interaction tables for Table 5,23.

Mean main stem length (cm)

Interactions significant to 1%

3-12-62

P x grass

Treatments	No P	P
No grass	1.81	4.76
Cut grass	1.65	2.68
Grass + clover	1.49	3.18
Uncut grass	1.65	2.70

P x N

Treatments	No P	P
No N	1.73	2.48
N	1.57	4.18

27-12-62P x grass

Treatments	No P	P
No grass	4.76	14.21
Cut grass	3.50	3.76
Grass + clover	2.34	4.30
Uncut grass	2.95	3.50

P x N

Treatments	No P	P
No N	4.04	4.94
N	2.73	7.95

25-1-63P x grass

Treatments	No P	P
No grass	14.21	34.81
Cut grass	7.18	4.80
Grass + clover	4.34	5.55
Uncut grass	5.02	3.99

P x N

Treatments	No P	P
No N	9.72	10.19
N	5.66	14.38

Final harvest (27-2-63)P x grass

Treatments	No P	P
No grass	32.52	46.45
Cut grass	12.75	8.00
Grass + clover	8.41	8.41
Uncut grass	5.98	4.84

P x N

Treatments	No P	P
No N	18.50	15.55
N	11.33	18.30

5,8. Interaction tables for Table 5,24.

Post-harvest soil moisture (% by volume)

Interactions significant to 1%

10-15 cm

P x grass

Treatments	No P	P
No grass	19.42	15.10
Cut grass	17.00	16.48
Grass + clover	17.36	16.70
Uncut grass	16.64	14.56

Moisture x grass

Treatments	Dry	Moist
No grass	13.06	21.46
Cut grass	9.76	23.71
Grass + clover	9.75	24.31
Uncut grass	8.82	22.38

18-23 cmP x grass

<u>Treatments</u>	<u>No P</u>	<u>P</u>
No grass	20.00	14.94
Cut grass	17.09	16.66
Grass + clover	17.65	16.98
Uncut grass	16.81	14.72

Moisture x grass

<u>Treatments</u>	<u>Dry</u>	<u>Moist</u>
No grass	13.49	21.45
Cut grass	9.81	23.94
Grass + clover	10.01	24.61
Uncut grass	8.82	22.71

40-45 cmP x grass

<u>Treatments</u>	<u>No P</u>	<u>P</u>
No grass	21.49	14.72
Cut grass	17.68	17.72
Grass + clover	18.95	17.74
Uncut grass	17.50	15.76

Moisture x grass

<u>Treatments</u>	<u>Dry</u>	<u>Moist</u>
No grass	14.44	21.78
Cut grass	10.05	25.35
Grass + clover	10.51	26.18
Uncut grass	8.92	24.34

6,1. Data to accompany Figure 6,7. Leaf area (cm²). n = 100 leaves.

N type brier

Field site	Mean area	Std. err.	C.V. %	S.E. of diff.	Prob-ability
Omarama	2.24	0.62	27.7		
Dry Creek	5.94	1.27	21.3	0.20	***
F. Hill	6.62	1.34	20.2	0.26	*
L. Pearson	7.37	1.32	18.0	0.26	*
Cora Lynn	8.30	1.82	21.9	0.33	*

A type brier

Dry Creek	3.85	1.03	26.7		
F. Hill	5.18	1.14	22.0	0.22	***
L. Pearson	6.07	1.70	25.6	0.29	**
Cora Lynn	7.17	1.50	20.8	0.32	**

6,2. Data to accompany Figure 6,8. Volume of hips (cc). N = 100 hips.

<u>N type brier</u>	Mean Vol.				
Dry Creek	1.34	0.23	17.1		
F. Hill sunny	1.03	0.22	22.3	0.031	***
F. Hill dark	1.67	0.24	14.3	0.032	***
L. Pearson	1.79	0.30	16.7	0.038	**
Cora Lynn	2.33	0.28	12.0	0.041	***

A type brier

Dry Creek	0.68	0.14	20.6		
F. Hill	0.60	0.14	23.3	0.020	***
L. Pearson	0.93	0.17	18.3	0.022	***
Cora Lynn	1.18	0.19	16.1	0.025	***

* (P < 0.05); ** (P < 0.01); *** (P < 0.001).