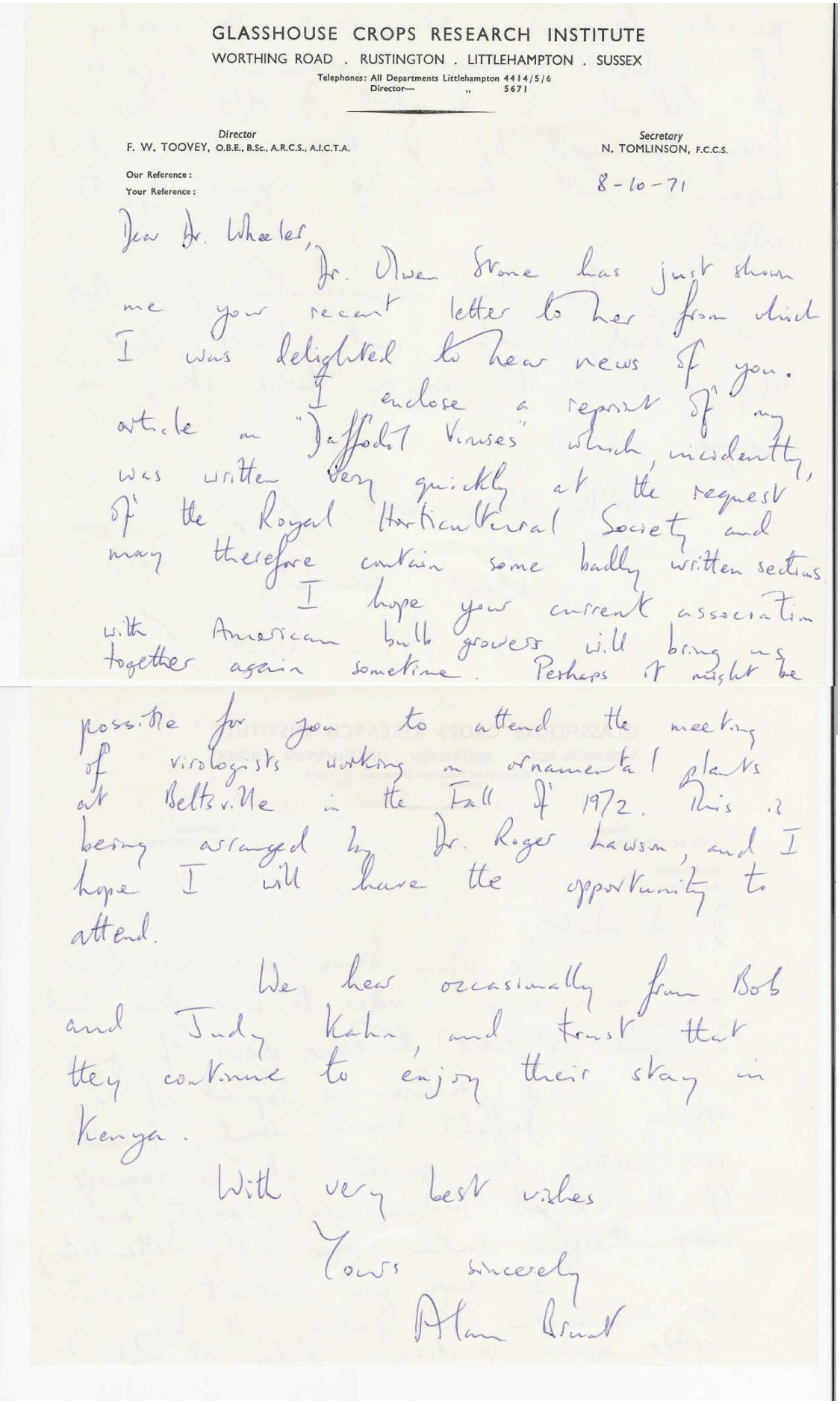


GLASSHOUSE CROPS RESEARCH INSTITUTE
WORTHING ROAD . RUSTINGTON . LITTLEHAMPTON . SUSSEX
Telephones: All Departments Littlehampton 4414/5/6
Director— " 5671

Director
F. W. TOOVEY, O.B.E., B.Sc., A.R.C.S., A.I.C.T.A.

Secretary
N. TOMLINSON, F.C.C.S.

Our Reference :
Your Reference :

8-10-71

Dear Dr. Wheeler,

Dr. Owen Stone has just shown me your recent letter to her from which I was delighted to hear news of you.

I enclose a reprint of my article on "Daffodil Viruses" which, incidentally, was written very quickly at the request of the Royal Horticultural Society and may therefore contain some badly written sections.

I hope your current association with American bulb growers will bring us together again sometime. Perhaps it might be possible for you to attend the meeting of virologists working on ornamental plants at Beltsville in the Fall of 1972. This is being arranged by Dr. Roger Lawson, and I hope I will have the opportunity to attend.

We hear occasionally from Bob and Judy Kahn, and trust that they continue to enjoy their stay in Kenya.

With very best wishes

Yours sincerely

Alan Brunt

Dear Dr. Wheeler,
Dr. Olivia Stone has just shown me your recent letter to her from which I was delighted to hear news of you.

I enclose a reprint of my article on "Daffodil Viruses" which, incidentally, was written very quickly at the request of the Royal Horticultural Society and may therefore contain some badly written sections.

I hope your current association with American bulb growers will bring us together again sometime. Perhaps it might be possible for you to attend the meeting of virologists working on ornamental plants at Beltsville in the Fall of 1972. This is being arranged by Dr. Roger Lawson, and I hope I will have the opportunity to attend.

We hear occasionally from Bob and Judy Kahn, and trust that they continue to enjoy their stay in Kenya.

With very best wishes,
Yours sincerely
Alan Brunt

VIRUS DISEASES OF NARCISSUS

A. A. Brunt

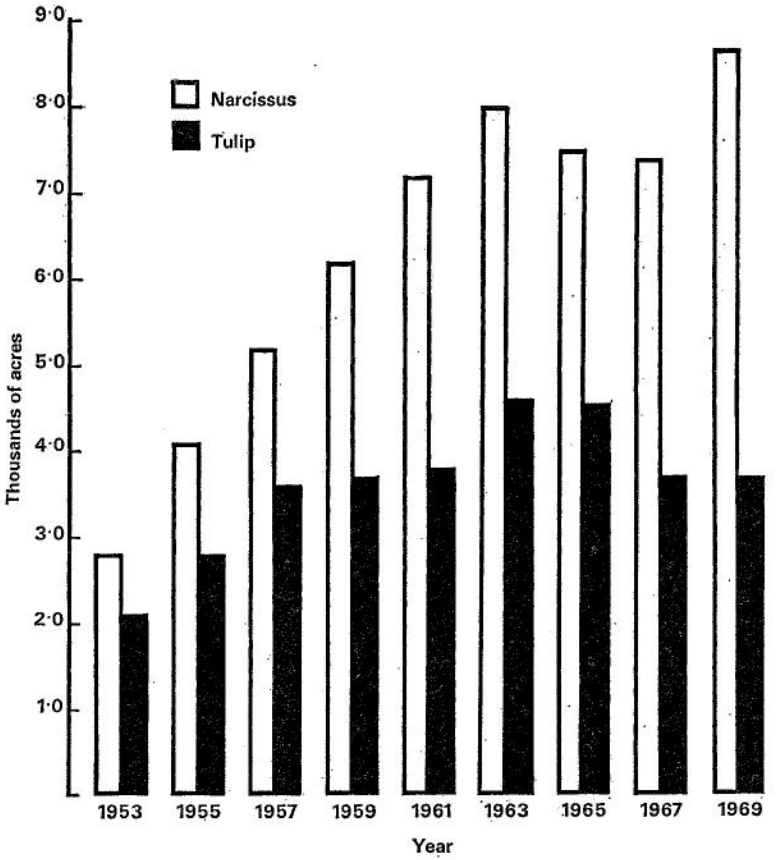
Glasshouse Crops Research Institute, Littlehampton, Sussex

FLOWERBULBS, especially narcissus and tulip, have long been among the most popular flowers grown by amateurs; they are now also very important crop plants in Britain, with an estimated commercial value of £16 million per annum. Between 1953 and 1969 the commercial acreage of tulips in England and Wales increased from about 2,100 to 3,700 acres while that of daffodils increased from 2,800 to almost 8,700 acres (Text Fig. 1); the area devoted to narcissus thus exceeds that of any other single ornamental crop in Britain and in 1965, the last year for which world production statistics are available (Gould, 1967), was much higher than the total acreages of other producing countries (see Text Fig. 2). This comparatively recent expansion of the bulb industry in Britain has been accompanied by increasing interest in all factors affecting productivity, and a wide range of problems is being investigated at the Glasshouse Crops Research Institute, the Scottish Horticultural Research Institute and at the National Agricultural Advisory Service Experimental Horticulture Stations at Rosewarne, Cornwall and Kirton, Lincolnshire.

Viruses occur commonly in narcissus and tulip; although some are relatively innocuous, others induce severe diseases which, if allowed to spread within crops, eventually cause considerable economic losses. Some virus-induced diseases are therefore of great importance to commercial growers and a cause of concern to amateurs, especially breeders, whose stocks may be small but very valuable. Moreover, because viruses may be distributed in bulbs exchanged and sold in world markets, interest in virus diseases is international.

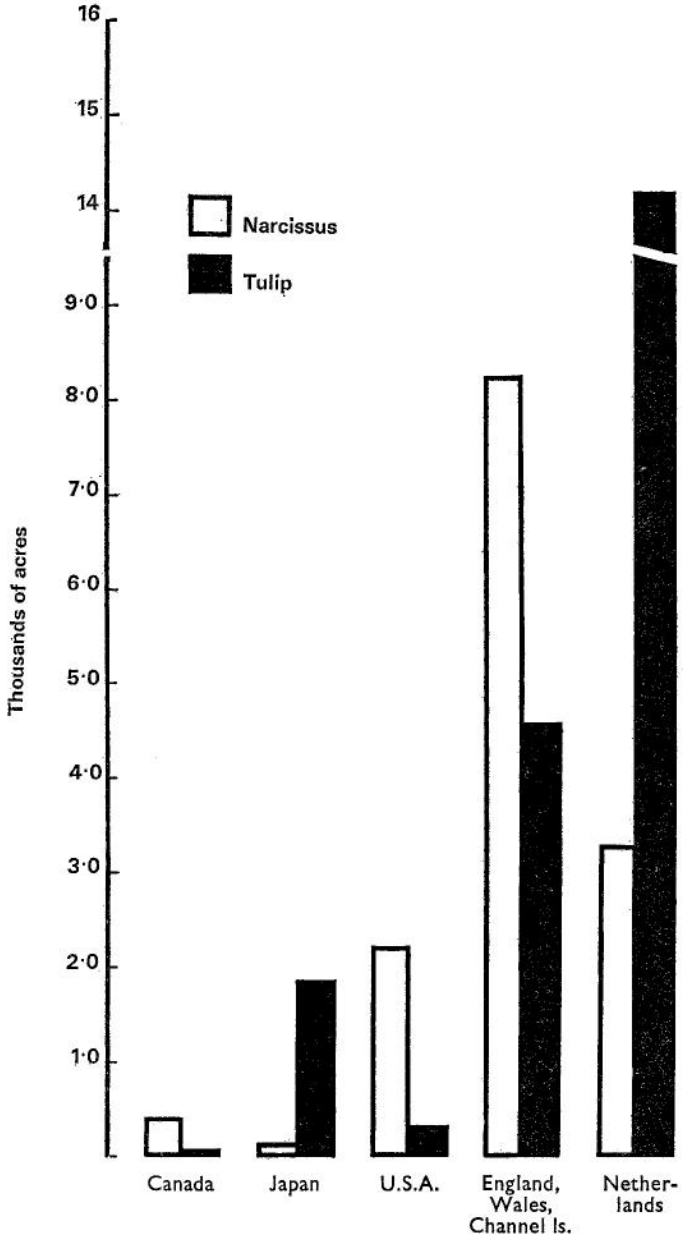
The virus diseases of tulips were reviewed in last year's Year Book (van Slogteren and Asjes, 1969). It is, perhaps, now an appropriate time to review current knowledge of those of narcissus since this was last done thoroughly in 1946 (van Slogteren and de Bruyn Ouboter, 1946) and in 1962 (Broadbent, Green and Walker, 1962).

Much less was known in 1962 about the viruses affecting narcissus than about those of many other crops. At that time many diseases had been recognised and variously named yellow stripe, green stripe, white streak, white stripe, silver streak, silver leaf, flower breaking, mottle,



Text Fig. 1. Acreage of daffodils and tulips grown in England and Wales 1953–1969.

mild mosaic, early maturity and decline, but most of the causal viruses had remained either unidentified or uncharacterised. Over the past seven years we have attempted at the Glasshouse Crops Research Institute to identify the causes of specific diseases, to characterise the viruses, to establish their symptomatology, importance and modes of spread, and to devise measures to limit their spread.



Text Fig. 2. World Bulb Production 1965 (statistics from Gould, 1967).

Viruses Infecting Narcissus

Like many other perennial or vegetatively-propagated crops, narcissus is susceptible to many plant viruses. Of the thirteen viruses presently recognized, six are transmitted by aphids, six are nematode-borne and the last has no known invertebrate vector (Table 1). Cucumber mosaic and the nematode-borne viruses all occur in a wide range of weed and cultivated plants in some crops causing economically important diseases; they have therefore previously attracted much attention and are now well-known, readily identifiable pathogens. By contrast, narcissus yellow stripe, narcissus white streak, narcissus latent, narcissus mosaic, jonquil mild mosaic and the 'Grand Soleil d'Or' virus are known to occur only in narcissus although narcissus yellow stripe virus occurs also in *Nerine* (Brunt, 1968).

Table 1. The viruses infecting daffodils

Viruses transmitted by		
Aphids	Nematodes	Mechanical methods
Narcissus yellow stripe	Arabis mosaic	Narcissus mosaic
Narcissus white streak	Strawberry latent ringspot	
Narcissus latent	Tomato black ring	
Grand Soleil d'Or virus	Raspberry ringspot	
Jonquil mild mosaic	Tobacco ringspot	
Cucumber mosaic	Tobacco rattle	

Survey results indicate that *N. jonquilla, N. tazetta* and *N. pseudo-narcissus* show differential susceptibility to some of these viruses (Table 2). Thus of several thousand diseased plants examined, narcissus white streak, narcissus mosaic and narcissus latent viruses have been found only in *N. pseudo-narcissus*, the 'Grand Soleil d'Or' virus only in *N. tazetta*, and jonquil mild mosaic only in *N. jonquilla*; narcissus yellow stripe virus induces similar symptoms in both *N. pseudo-narcissus* and *N. jonquilla*, but does not occur in *N. tazetta*. *N. tazetta* has never been found infected with tobacco rattle virus even when grown in areas where spread of this virus is rapid among plants of *N. pseudo-narcissus*.

Cucumber mosaic virus, although occurring commonly in *N. tazetta*, has been found only rarely in *N. pseudo-narcissus*. The soil-borne ringspot viruses (arabis mosaic, strawberry latent ringspot and tomato black ring) however, infect both *N. tazetta* and *N. pseudo-narcissus*.

Table 2. Differential susceptibility of Narcissus species to different viruses

Virus	*N. pseudonarcissus*	*N. tazetta*	*N. jonquilla*
Narcissus yellow stripe	+	—	+
Narcissus latent	+	—	—
Narcissus mosaic	+	—	—
Narcissus white streak	+	—	—
Arabis mosaic	+	+	—
Raspberry ringspot	+	—	—
Strawberry latent ringspot	+	+	—
Tomato black ring	+	+	—
Tobacco rattle	+	—	—
Cucumber mosaic	+	+	—
Soleil d'Or virus	—	+	—
Jonquil mild mosaic	—	—	+

Tobacco ringspot virus is omitted from this list because its occurrence in daffodils has been reported only recently, and *N. tazetta* and *N. jonquilla* have not yet been adequately tested.

Little is yet known about jonquil mild mosaic virus, but each of the other viruses occurring in daffodils is briefly considered below.

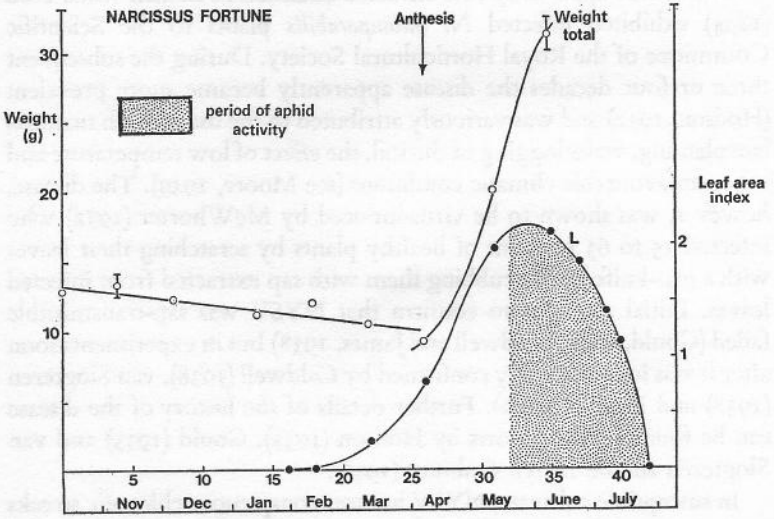
Aphid-borne Viruses

Some of the most important viruses affecting daffodils are aphid-borne. Of the six, cucumber mosaic is the only one which also occurs in numerous other plant species and can be transmitted by many different aphid species (Kennedy, Day and Eastop, 1962); infection in daffodils can therefore originate from other infected daffodils or, more likely, from any of many other potential sources. By contrast, the remaining viruses probably spread only from infected to healthy daffodils, although *Nerine* might sometimes be a primary source of infection of narcissus yellow stripe virus.

As daffodils are rarely colonised by wingless aphids (Apterae) in Britain, some growers find it difficult to accept that narcissus viruses are

aphid-borne. Failure of aphids to colonise, however, is probably due to unfavourable environmental conditions during most of the daffodil growing season, because infestation has been observed under more favourable climatic conditions; colonies of *Macrosiphum euphorbiae* have been found in daffodils grown on Long Island, New York (Blanton and Haasis, 1942), and *Aphis fabae* has been found on daffodils in Holland grown during late summer for export to South Africa, South America and Australia (van Slogteren and de Bruyn Ouboter, 1946).

Although winged aphids (Alatae) are also rarely seen feeding on daffodils, Broadbent, Green and Walker (1962) operated insect traps in small narcissus plots in southern England from April to mid-July for three years (1953–55) and demonstrated unequivocally that, although so rarely seen, substantial numbers of Alatae visit daffodils. Another significant feature of this investigation was the failure to trap any aphids before mid-May in any year; thus, as the daffodil season normally extends only to the middle or end of July, exposure to aphids and spread of aphid-borne viruses can normally occur only during a period of about six to eight weeks. This is illustrated in Text Figure 3 which indicates the normal seasonal growth of 'Fortune' daffodil with, superimposed, the relatively brief period during which they are "at risk" to aphids.



Text Fig. 3. Seasonal growth of Narcissus 'Fortune' in S. England with, superimposed, the period coinciding with the occurrence of aphids. From A. R. Rees "Physiology of ornamental bulbous plants" (in preparation).

Like narcissus yellow stripe and narcissus latent, the remaining aphid-borne viruses are probably not seed- or pollen-borne and are not highly infectious. Moreover, unlike tulip breaking and cucumber mosaic viruses in tulip, it is unlikely that aphids spread virus from infected to healthy bulbs during storage. Narcissus yellow stripe, narcissus latent and cucumber mosaic viruses are known to be acquired and transmitted by aphids within a few minutes (so-called "stylet-borne" or "non-persistent" viruses), and the size and shape of narcissus white streak, jonquil mild mosaic and 'Grand Soleil d'Or' viruses suggest that they too are stylet-borne. There are many indications, therefore, that migratory aphids are solely responsible for the field spread of these six viruses.

Narcissus yellow stripe virus (*NYSV*)

Symptomatology and occurrence

Narcissus yellow stripe, the longest-known narcissus virus disease, was recognized in the Netherlands (van Slogteren and de Bruyn Ouboter, 1946) and Britain (Dod, 1894) during the nineteenth century, and is still probably the most important disease. It probably now occurs wherever daffodils are grown (Moore, 1949), presumably because of past international trade in partially-infected bulb stocks.

The disease apparently first attracted attention in Britain when Dod (1894) exhibited infected *N. incomparabilis* plants to the Scientific Committee of the Royal Horticultural Society. During the subsequent three or four decades the disease apparently became more prevalent (Hodson, 1932) and was variously attributed to the use of fresh manure, late planting, waterlogging of the soil, the effect of low temperature and other unfavourable climatic conditions (see Moore, 1949). The disease, however, was shown to be virus-induced by McWhorter (1932) who infected 35 to 63 per cent of healthy plants by scratching their leaves with a pen-knife before rubbing them with sap extracted from infected leaves. Initial attempts to confirm that NYSV was sap-transmissible failed (Gould, 1935; Caldwell and James, 1938) but in experiments soon after it was independently confirmed by Caldwell (1938), van Slogteren (1938) and Haasis (1939b). Further details of the history of the disease can be found in the reports by Hodson (1932), Gould (1935) and van Slogteren and de Bruyn Ouboter (1946).

In susceptible cultivars, NYSV induces conspicuous chlorotic streaks on leaves and flower stalks, distortion and curling of leaves, and "breaking" of flowers; the growth and yield of infected plants is progressively and severely reduced. Some cultivars are more tolerant

and exhibit less conspicuous symptoms. A full description of the disease is unnecessary because the symptoms must be familiar to all growers, and those occurring on numerous cultivars, moreover, have been fully described and illustrated by van Slogteren and de Bruyn Ouboter (1946) and by Caldwell and Kissick (1949).

Transmission

Unlike many other aphid-borne plant viruses, NYSV spreads only slowly. Spread was earlier attributed to contact between the roots of infected and healthy daffodils (McWhorter, 1932; Hawker, 1943), to contact during hot-water treatment, to thrips (Hodson, 1932) and to the handling of infected and healthy plants during flower harvesting (Ryan, 1929). Present evidence strongly suggests, however, that aphids are the most important, and probably the sole natural mode of spread.

Under experimental conditions, up to 70 to 80 per cent of plants inoculated with sap from diseased plants become infected. Nevertheless, it is very unlikely that the virus is sufficiently infectious to be spread by alternately handling infected and healthy plants during harvesting flowers or other cultural operations; McWhorter and Weiss (1932) and Haasis (1939b) failed to detect spread in field experiments where healthy and diseased flowers were harvested alternately, and were thus unable to confirm an earlier report that this was possible. In similar tests performed in glasshouses, however, Haasis (1939b) detected a very low rate of transmission, which suggests that spread may occur under forcing conditions; this, however, would be of no importance because forced bulbs are usually discarded after flowering.

Aphids were first shown to be the vectors of NYSV by Blanton and Haasis: in 1939 they demonstrated that *Acyrthosiphon solani* (glasshouse-potato aphid), *Aphis fabae* (black bean aphid) and *Macrosiphum euphorbiae* (potato aphid) were vectors on Long Island, New York, and in 1940 and 1942 they reported that *Acyrthosiphon pisum* (pea aphid), *Dysaphis plantaginea* (rosy apply aphid), *Macrosiphum rosea* (rose aphid) and *Myzus cerasi* (cherry black fly) were also able to transmit. The ability of *A. solani, A. fabae* and *M. euphorbiae* to transmit NYSV was confirmed in the Netherlands by van Slogteren and de Bruyn Ouboter (1946) who found that *Neomyzus circumflexus* (mottled arum aphid) and *Rhopalosiphoninus staphyleae* (mangold aphid) were also able to transmit. Thus nine aphid species are known to be vectors. In recent tests with *A. pisum*, NYSV was found to be acquired and transmitted within a few minutes and is thus a stylet-borne or "non-persistent" virus.

NYSV usually spreads slowly and often only to neighbouring plants

(Hawker, 1943; van Slogteren and de Bruyn Ouboter, 1946); this pattern of spread, which at one time was difficult to interpret, is now known to be associated with the short period of vector activity and is typical of some "non-persistent" viruses (Broadbent *et al.*, 1962).

From their aphid-trapping experiments, Broadbent *et al.* (1962) clearly showed that the rate of spread was proportional to the relative abundance of aphids during the previous season. Moreover, van Slogteren and de Bruyn Ouboter (1946) have observed that infection rates were 41 to 72 per cent higher in daffodils lifted four to eight weeks later than usual; this increased rate of spread is undoubtedly due to the longer period of exposure to aphids. The rate of spread also increased in proportion to the number of infected plants present within stocks; thus in plots originally containing 10, 20 and 50 per cent infected plants, over a period of three years 16, 46 and 90 per cent respectively, of the originally healthy plants became infected (Haasis, 1939b; Broadbent *et al.*, 1962).

Properties of the virus

Although sap-transmissible to narcissus from narcissus and *Nerine*, NYSV has failed in our experiments to infect any of about 30 herbaceous plants which are susceptible to a wide range of different plant viruses.

NYSV particles are flexuous filaments (Cremer, van Slogteren and van de Veken, 1960) which are *ca.* 755 nm long (1,000,000 nm = 1 mm) and readily detected by examining suitably-treated sap in an electron microscope. In the absence of herbaceous indicator plants therefore, electron microscopy has proved particularly useful for rapidly detecting NYSV and other, shorter filamentous narcissus viruses (Brunt and Atkey, 1967). Serological tests, however, are necessary for specifically identifying viruses.

Narcissus white streak virus (*NWSV*)

Symptomatology and occurrence

A virus disease briefly described as "silver streak" in Britain in 1933 (Chittenden, 1933) is probably identical with that later described in greater detail and named "white streak" or "white stripe" in the U.S.A. (McWhorter, 1938 & 1939; Haasis, 1939a) and as "silver leaf" (*zilverblad*) in the Netherlands (van Slogteren and de Bruyn Ouboter, 1946). Haasis (1939a) first fully described the disease, and his name "white streak" is probably the most appropriate. Unlike plants infected with NYSV, those infected with NWSV usually remain symptomless until

three to four weeks or more after flowering. Leaves and flower stalks then develop purple longitudinal streaks which later become white and often coalesce; within a few days the streaks become necrotic and sunken, and the leaves soon die. This abnormally early senescence at first led McWhorter (1938) to call the disease "early maturity" or "early decline", the latter a name he still prefers (McWhorter, 1957). Symptoms on leaves have been amply described and illustrated by Haasis (1939a) and van Slogteren and de Bruyn Ouboter (1946). Laboratory tests in the U.S.A. (Haasis, 1939a), recently confirmed at the Glasshouse Crops Research Institute (Brunt, 1968), have shown that the development of symptoms is delayed until temperatures exceed 18°C; thus in Britain it is unusual to observe symptoms before the middle of May. As premature senescence occurs at a time when environmental factors are most favourable for photosynthesis and the accumulation of dry matter by bulbs, infection can reduce bulb yield by 30 to 40 per cent within two to four years (McWhorter, 1957). Because of the rapid onset of the disease, virus-induced senescence is possibly often mistaken for normal senescence; NWSV is therefore potentially one of the most important viruses infecting daffodils.

Transmission

Blanton (1939) found that on Long Island, New York, NWSV is efficiently transmitted from infected to healthy daffodils by *Aphis fabae* and *Macrosiphum euphorbiae*, two species which are also vectors of NYSV. Van Slogteren and de Bruyn Ouboter (1946) later confirmed that *A. fabae* was a vector of NWSV in the Netherlands and reported that the virus was also efficiently transmitted by *Myzus persicae* and *Acyrthosiphon pisum*. At about the same time Haasis (1939a) showed that NWSV was also transmissible by sap inoculation. The virus, however, is not highly infectious and, like NYSV, aphids are probably solely responsible for its spread.

Properties of the virus

The particles of NWSV are flexuous filaments which, like those of NYSV, mostly measure about 750 nm (Brunt, 1969). These particles occur in fairly high concentration in infected plants and can be readily detected by examining infective sap in an electron microscope.

Narcissus is the only known host of this virus, my attempts to infect any of 25 mechanically inoculated herbaceous plant species so far proving unsuccessful. The virus is purified with some difficulty, and needs to be further characterized.

Although NYSV and NWSV particles are similar in shape and size, they are probably distinct viruses. Thus the greenish or yellowish leaf symptoms induced by NYSV often appear soon after leaf emergence, often consist of raised and roughened outgrowths which persist until "masked" by high temperatures; by contrast, the white streaks induced by NWSV first appear three to four weeks or more after flowering, are intensified at high temperatures (up to 18°C), and consist of dead and sunken epidermal and parenchyma tissues. Moreover, 'Golden Harvest' plants infected with both viruses produce a mixture of yellow stripe and white streak symptoms, whereas those infected with either virus alone produce only one type of symptoms.

Narcissus latent virus (*NLV*)

Occurrence

A hitherto undescribed virus, subsequently named narcissus latent virus, was first found infecting narcissus during investigations on NYSV and NWSV (Brunt and Atkey, 1967). This virus is prevalent in many cultivars, probably because it induces only inconspicuous symptoms and has spread unrecognized for many years.

The virus has been detected in plants of 'Lucifer', 'Magnificence', 'Cheerfulness', 'Tinker', 'Rembrandt', 'Spanish Gold', 'Scarlet Elegance', 'Minister Talma' and 'Criterion', all of which, however, were infected also with narcissus yellow stripe or narcissus mosaic viruses. NLV only, however, was detected in several plants of 'Glorification', some of which were symptomless but others having very mild chlorotic areas on leaves.

Transmission

NLV has so far failed to infect any of about 25 plant species that are unrelated to narcissus, but is readily transmitted from infected to healthy daffodils by mechanical inoculation and by the pea aphid (Brunt, 1968).

Properties of the virus

Specific antisera to NLV are readily prepared and have proved particularly useful for its rapid detection and identification. The particles of NLV are filamentous and measure about 650 nm (Brunt, 1968). Viruses of similar shape and size occur in a wide range of weed and cultivated plants. However, NLV appears to be a distinct virus because in my serological tests it has shown no relationship to morphologically-similar viruses occurring in potatoes, carnations, chrysanthemums and cowpeas.

'Grand Soleil d'Or' virus (SoDV)

Occurrence

The cultivar 'Grand Soleil d'Or' is widely grown on the Isles of Scilly and is said to have degenerated considerably over the past three or four decades. This decline may have had several contributory causes, but as virus infection is prevalent in this cultivar it is likely that viruses are associated with the loss of vigour and productivity. Five viruses commonly occur in it, often in complexes (Brunt, 1966a). Of these, tomato black ring, arabis mosaic and strawberry latent ringspot are possibly the least important; also prevalent, and probably of greater importance, are cucumber mosaic and another virus tentatively named 'Grand Soleil d'Or' virus which is apparently distinct from those occurring in trumpet daffodils. The leaves of infected plants produce conspicuous yellow stripes and general chlorosis but, because such naturally-infected plants have always contained other viruses, it has previously proved impossible to establish the symptomatology of each. Until recently no virus-free plants of this cultivar were available; however, my colleague Dr. O. M. Stone has recently obtained virus-free plants by meristem-tip culture techniques (Stone, 1969), and these will be used to establish the symptomatology of the five viruses and, more importantly, to confirm that aphids are responsible for the spread of SoDV.

Properties of the virus

SoDV has flexuous filmentous particles which, like those of NYSV and NWSV, are *ca* 750 nm long (Brunt, 1968); although it has so far failed to infect any of numerous dicotyledonous indicator species, SoDV can be readily identified by serological methods (Brunt, 1969).

The morphology and properties of the virus suggest that, like NYSV and NWSV, it is a member of the potato virus Y group. The virus is therefore probably transmitted from infected plants by aphids, although this has yet to be confirmed. Preliminary tests have so far failed to detect any relationship between SoDV and several morphologically-similar viruses (Brunt, 1969).

Cucumber mosaic virus (CMV)

CMV is the only aphid-borne virus affecting daffodils which has a wide natural host range. It occurs commonly in 'Grand Soleil d'Or', invariably together with other viruses, but only rarely in trumpet daffodils (Brunt, 1966a). Although its symptomatology is unknown it is, however, readily isolated and identified.

The main characteristics of this and other aphid-borne viruses are presented in Table 3.

Nematode-borne Viruses

The six nematode-borne viruses occur in a wide range of weed and cultivated species and have been intensively studied over the past decade. They can thus be readily isolated and subsequently identified by host-plant and serological reactions, and by their characteristic properties. As narcissus is merely one of numerous hosts of these viruses, infection in daffodils can occur both from within narcissus crops and from outside sources, and infected daffodils can also act as reservoirs of infection for other more susceptible crops.

The viruses are probably transmitted to narcissus by those nematodes responsible for their spread in other crops: tobacco rattle virus by *Trichodorus* species, and the others by *Longidorus* or *Xiphinema* species.

Tobacco rattle virus (TRV)

TRV, first recognized as a pathogen of narcissus and other flowerbulbs in the Netherlands (van Slogteren, 1958), was later found during a survey in Britain in 10 of 45 commercial stocks and in 1 of 79 new cultivars (Brunt, 1966a) often in complex with other viruses. 'Minister Talma' plants infected with TRV remain symptomless, but 'Golden Harvest' and 'Thalia' produce leaf symptoms indistinguishable from those of the "mottle" disease described earlier by Broadbent *et al.* (1962); 'Grand Soleil d'Or' is apparently immune to TRV, for infection has not been detected in any of the numerous samples grown in areas containing both the vector and infected plants and where the virus spreads fairly rapidly into trumpet daffodils.

Soil-borne ringspot viruses

Raspberry ringspot virus occurs in Scotland, and has been found infecting daffodils there by Mr. W. P. Mowat (personal communication). Arabis mosaic (AMV), strawberry latent ringspot (SLRV) and tomato black ring (TBRV) occur in both trumpet daffodils and 'Grand Soleil d'Or' (Brunt, 1966a). In the latter AMV is prevalent but, probably like TBRV and SLRV which occur more rarely, is apparently symptomless.

AMV and TBRV were first isolated from daffodils in Scotland and S.W. England by Todd and Jenkins (Broadbent *et al.*, 1962). Although TBRV has not yet been isolated from trumpet daffodils, AMV was isolated from 'Golden Harvest', 'Killymore', 'King Alfred', 'Gog' and

Table 3. The main characteristics of the aphid-borne viruses occurring in Narcissus

Virus	Diseases induced	Hosts	Transmitted by	Importance	Particle size + morphology
Narcissus yellow stripe	Yellow stripe, greys or "grijs", flower breaking, ? green stripe	*N. pseudo-narcissus*, *N. jonquilla* and *Nerine*	Glasshouse/potato, black bean, potato, pea, rosy apple, rose, cherry black fly, mottled arum and mangold aphids	Very damaging; prevalent only in badly maintained stocks	Filamentous, 750 × 12 nm
Narcissus white streak	White streak, white stripe, early maturity, decline, "Zilverblad"	*N. pseudo-narcissus*	Black bean, potato, pea, and potato/peach aphids	Very damaging, prevalent occasionally	Filamentous, 750 × 12 nm
Narcissus latent	Inconspicuous symptoms only	*N. pseudo-narcissus*	Pea aphid	Prevalent but relatively unimportant	Filamentous, 650 × 14 nm
'Grand Soleil d'Or'	Associated with leaf chlorosis and decline	*N. tazetta*	? Pea aphid	Prevalent and possibly very damaging	Filamentous, 750 × 12 nm
Jonquil mild mosaic	Mild mosaic	*N. jonquilla*	? Pea aphid	Prevalent but of slight importance	Filamentous, 820 × 12 nm
Cucumber mosaic	Symptomless in *N. pseudo-narcissus* ? Mosaic in *N. tazetta*	Numerous plant species	Numerous species	Rare in trumpet daffodils. Prevalent in 'Grand Soleil d'Or'	Isometric, 28-30 nm

'Fortune' plants, but SLRV was isolated from only two narcissus stocks (Brunt, 1966a). Daffodil seedlings artificially infected with AMV, TBRV and SLRV, however, showed no conspicuous symptoms; the three viruses thus seem to be less important than the aphid-borne viruses.

A strain of tobacco ringspot virus (TRSV) was first found infecting narcissus in the Netherlands (Asjes, 1969). This virus is occasionally detected in gladioli and other susceptible crops imported into Europe, and has hitherto been thought to be endemic only in North America where the vector is known to be *Xiphinema americanum*; its incidence in daffodils, tulips, irises and hyacinths suggests that spread probably occurs also in the Netherlands, although the vector there has yet to be identified. As TRSV has such an extensive host range, infected daffodils could well be important as reservoirs of infection for other more susceptible crops.

Narcissus Mosaic Virus (NMV)—A virus without a known invertebrate vector

Occurrence and importance

Just before the outbreak of World War II van Slogteren and de Bruyn Ouboter (1946) distinguished a mosaic disease caused by NMV from the long-known "yellow stripe" or "greys" disease, and the two viruses were later briefly reported to differ serologically (van Slogteren, 1955) and morphologically (Cremer and van der Veken, 1964). Unfortunately "narcissus mosaic virus" had previously been widely used as a synonym for narcissus yellow stripe virus in the U.S.A. (e.g. Haasis, 1939b; McWhorter, 1932; Blanton and Haasis, 1942) and, rarely, in Britain (Caldwell, 1946). That one name had earlier been used simultaneously for two distinct viruses has caused some confusion; however, this can easily be avoided if "narcissus yellow stripe" is reserved for the virus causing conspicuous yellow stripe symptoms and having the properties described earlier, and if "narcissus mosaic virus" is retained for the more stable virus inducing only a mild mosaic disease in narcissus (Brunt, 1966b).

NMV is prevalent in trumpet daffodils; in a preliminary survey, NMV was isolated from plants in 27 of the 48 commercial daffodil stocks tested, but from none of those in 10 'Grand Soleil d'Or' (*N. tazetta* L.) and 2 jonquil (*N. jonquilla* L.) stocks although both the latter species contained other viruses. Plants of the following commercial cultivars were infected: 'Actaea', 'Aranjuez', 'Brunswick', 'Carlton', 'Cheerfulness', 'Fortune', 'Golden Harvest', 'Inglescombe', 'King Alfred', 'Magnificence', 'Minister Talma', 'Mount Hood', 'Royal Bride' and 'Zero'. With the exception of 'Actaea' (*N. poeticus*) all

infected cultivars are trumpet, large-cupped or double narcissi of garden origin (Division 1, 2 and 4, respectively; Anon., 1969). Some of the older, widely grown cultivars such as 'Fortune', 'Golden Harvest'. 'Magnificence' and 'King Alfred' are apparently wholly infected because NMV was found in all samples from several different stocks of each. The incidence in other cultivars was also high. NMV was also obtained from 31 of the 79 new cultivars in the Narcissus Trial at the R.H.S. Garden, Wisley.

Most narcissus plants in which NMV was the only virus detected were either symptomless or developed inconspicuous mosaic symptoms at the bases of leaves during and after flowering. NMV-infected 'Minister Talma' plants were exceptional in producing distinct mosaic symptoms that differed from those caused by NYSV.

To establish the symptomatology of NMV, fifty-eight five-year-old virus-free narcissus seedlings (from open-pollinated 'King Alfred' and 'Sulphur' plants) were inoculated when leaves were 10–18 cm long using highly infective purified preparations of NMV made from *Gomphrena globosa*; another 34 'Sulphur' seedlings were inoculated with infective sap from crimson clover. No symptoms appeared during the following eight months, and attempts to re-isolate NMV from the inoculated plants failed. About 17 months after inoculation, all developed inconspicuous mosaic symptoms at the bases of leaves, and virus was then recovered from inoculated plants. Flowers on infected seedlings were symptomless (Brunt, 1966*b*).

Properties of the virus

Unlike the aphid-borne filamentous viruses, NMV is readily transmitted to herbaceous indicator plants and subsequently identified. In one investigation, it infected 28 of the 53 species inoculated, the most useful test plants being *Gomphrena globosa, Tetragonia expansa, Nicotiana clevelandii* and *Chenopodium amaranticolor* (Brunt, 1966b).

Attempts to transmit NMV by aphids (*Aphis fabae, Acyrthosiphon pisum* and *Myzus persicae*) have so far failed. The virus is, however, highly infectious and is thus probably spread by handling.

The virus particles are flexuous filaments which, unlike those of other narcissus viruses, measure about 550 nm. NMV thus resembles viruses of the potato virus X group in general properties, size and shape of particles and in lacking an arthropod vector. Serological tests, however, have so far failed to detect any serological relationship between NMV and seven of these viruses; NMV thus appears to be a distinct virus.

Conclusions

Over the past three or four decades much has been learnt about the virus diseases of narcissus, yet the more severe diseases still cause concern to both commercial and amateur growers. As bulbs are vegetatively propagated, all offspring from infected plants are likely to be infected; moreover, unlike some bacteria and fungi, viruses cannot be eliminated from infected bulbs by chemotherapy or heat. In the absence of simple curative treatments, therefore, the importance of viruses can best be minimized by limiting their spread. Although there is little that can be added to previous recommendations, it is perhaps worthwhile restating briefly those methods which have proved simple and effective.

The most important and obvious method of control, roguing infected plants, is supported by much experimental evidence and its continuance must form the basis of any control programme. As the important aphid-borne viruses induce conspicuous leaf symptoms, infected plants can be readily recognized and removed before aphids occur in large number; plants infected with narcissus yellow stripe virus should be rogued during March and April, and those with narcissus white streak virus in late May. Similarly, spread of the nematode-borne tobacco rattle virus should be minimized by roguing infected plants early in the season before higher soil temperatures favour the reproduction and movement of the eelworm vectors.

As in some other plant species, the soil-borne ringspot viruses are seed-borne in narcissus; cucumber mosaic virus is also seed-borne in some species, but has not been demonstrated to occur in daffodils. None of the other viruses, however, is pollen- or seed-borne, and all aphid and nematode-borne viruses are insufficiently infectious to be transmitted by alternately handling infected and healthy plants.

As the aphid-borne viruses are all stylet-borne, winged aphids are able to transmit viruses to healthy plants within seconds of feeding on infected plants. Control of the aphid vectors, however, has proved difficult; spraying with systemic insecticides apparently increased the rate of spread in small plots (Broadbent, Green and Paton, 1957), presumably because treated plants are unpalatable and this leads to greater activity of the feeding aphids immediately before their death. It remains to be tested whether similar higher rates of spread would occur under similar conditions within large fields, or whether even a temporary increase in the movement of Alatae would result in less spread than would occur during uncontrolled prolonged visits by the vectors. It is sometimes possible to minimize the spread of nematode-borne viruses

by avoiding the use of ground suspected of harbouring the viruses and their vectors. If this is not possible the eelworm populations can be drastically reduced by treating the soil with various chemicals such as D-D (dichloropropane-dichloropropene), quintozene, methyl bromide and dichlorobromopropane. Such soil treatment, however, is costly and may be justified only where the viruses and their vectors are especially prevalent or where unusually valuable stocks are being grown.

Under appropriate circumstances, growing plants in isolation is often advantageous. Thus newly-purchased stocks should be considered suspect and grown in isolation until proved to have a lower incidence of infection than established stocks. Similarly, improved stocks can be obtained by selecting the most vigorous plants and bulking them up in isolation from normal commercial stocks; this, perhaps, as in the carnation, chrysanthemum, strawberry and other industries, might best be done by specialist contractors or growers with the requisite facilities.

Many commercial growers are, of course, well aware of the importance of these major control measures. The high incidence of viruses in new cultivars, mostly raised by amateurs, suggests that some amateur growers are less aware of viruses and their effects on growth and yield. This unawareness can sometimes lead to much disappointment as 15 or 20 years' effort and cost in breeding a new cultivar may be wasted if toward the end of this period the cultivar becomes totally infected. Breeders, therefore, can make a great contribution by ensuring that potentially-valuable seedlings are raised under conditions which will preclude or greatly reduce the possibility of infection occurring. This can be done very cheaply; by growing bulbs in sterilized compost under simple wooden cages covered with a fine mesh (32 mesh Tygan is adequate) to exclude aphids, both nematode and aphid-borne viruses can be avoided.

REFERENCES

ANON. (1969) Classified list of daffodil names. *Royal Horticultural Society, London.* Pp. 374.

ASJES, C. J. (1969) Virusziekten in Narcissen. *Jaarverslag (Annual Report), Laboratorium voor Bloembollenonderzoek, Lisse 1968–1969.*

BLANTON, F. S. (1939). Aphid transmission of the virus causing white streak of Narcissus. *J. econ. Ent. 32:* 726–7.

BLANTON, F. S. and F. A. HAASIS (1939) Transmission of narcissus mosaic virus by aphids. *J. econ. Ent. 32:* 469–70.

BLANTON, F. S. and F. A. HAASIS (1940) Three additional species of aphids transmitting narcissus mosaic. *J. econ. Ent. 33:* 942.

BLANTON, F. S. and F. A. HAASIS (1942) Insect transmission of the virus causing narcissus mosaic. *J. agric. Res. 65:* 413–9.

BROADBENT, L., D. E. GREEN, and J. B. PATON (1957) Virus diseases in the narcissus trial at Wisley. *J. Roy. hort. Soc. 82:* 395–401.

BROADBENT, L., D. E. GREEN and P. WALKER (1962) Narcissus virus diseases. *Daffodil and Tulip Year Book 28:* 1–7.

BRUNT, A. A. (1966a) The occurrence of cucumber mosaic and four nematode-transmitted viruses in British narcissus crops. *Pl. Path. 15:* 157–60.

BRUNT, A. A. (1966b) Narcissus mosaic virus. *Ann. appl. Biol. 58:* 13–23.

BRUNT, A. A. (1968) Narcissus viruses. *Rep. Glasshouse Crops Res. Inst. 1967:* 102–3.

BRUNT, A. A. (1969) Narcissus viruses. *Rep. Glasshouse Crops Res. Inst. 1968:* 105–6.

BRUNT, A. A. and P. T. ATKEY (1967) Rapid detection of narcissus yellow stripe virus and two other filamentous viruses in crude negatively-stained narcissus sap. *Rep. Glasshouse Crops Res. Inst. 1966:* 155–69.

CALDWELL, J. (1946) Mosaic disease of the Narcissus. *Nature, Lond. 158:* 735.

CALDWELL, J. and A. L. JAMES (1938) An investigation into the "stripe" disease of Narcissus. I. The nature and significance of the histological modifications following infection. *Ann. appl. Biol. 25:* 244–53.

CALDWELL, J. and E. KISSICK (1950) Varietal response to narcissus stripe. *Daffodil and Tulip Year Book 16:* 64–74.

CHITTENDEN, F. J. (1933) Mosaic disease of narcissi. *Daffodil Year Book 4:* 72–3.

CREMER, M. C., D. H. M. VAN SLOGTEREN, and J. A. VAN DER VEKEN (1960) Intracellular virus inclusions in leaves of 'grey diseased' Narcissus. *Proc. Eur. Reg. Conf. Electron Microsc., Delft, 1960.* (Ed. A. L. Houwink and B. J. Spit) *2:* 974–7.

DOD, C. WOLLEY (1894) Variegation in Narcissus. *Gdnrs' Chron. 15:* 507.

GOULD, C. J. (1967) World production of bulbs. *Florists' Review 140:* 14–16, 70–1.

GOULD, N. K. (1935) "Stripe" disease of daffodils. *J. Roy. hort. Soc. 60:* 492–500.

HAASIS, F. A. (1939a) White streak of Narcissus. *Phytopathology 29:* 890–5.

HAASIS, F. A. (1939a) Studies on narcissus mosaic. *Mem. Cornell Univ. agric. Exp. Sta. 224,* pp. 22.

HAWKER, L. E. (1943) Experiments on the spread of "narcissus stripe" in the field. *Ann. appl. Biol. 30:* 184–5.

HODSON, W. E. H. (1932) Narcissus pests. *Bull. Min. Agric. Fish. London. 51,* 31–33.

KENNEDY, J. S., M. F. DAY, and V. F. EASTOP (1962) A conspectus of aphids as vectors of plant viruses. *Commw. Inst. Entom., London.* Pp. 114.

MCWHORTER, F. P. (1932) Narcissus 'gray disease' is a transmissible mosaic. *Florists' Exchange 79:* 11.

MCWHORTER, F. P. (1938) Narcissus mosaic and early maturity. *Plant Dis. Rptr 22:* 147–8.

McWHORTER, F. P. (1939) The white streak or white stripe disease of Narcissus. *Phytopathology* (Abs.) *29:* 826.

McWHORTER, F. P. (1957) Bulb growing and forcing. *Northwest Bulb Growers Association Handbook, U.S.A.,* 127–30.

McWHORTER, F. P. and F. WEISS (1932) Diseases of Narcissus. *Bull. Oregon State agric. Exp. Sta.* 304: 16–32.

MOORE, W. C. (1949) Diseases of bulbs. *Bull. Min. Agric. Fish. 117.* H.M. Stationery Office, London. Pp. 176.

RYAN, H. J. (1929) Mosaic disease infecting bulb plantings in Los Angeles County. *California Agric. Dept. Monthly Bull. 18:* 293.

STONE, OLWEN M. (1969) Virology. Bulb plants. *Rep. Glasshouse Crops Res. Inst. 1968,* 110.

VAN SLOGTEREN, E. (1938) The transmission of virus diseases in daffodils. *Chronica Botanica 4:* 205.

VAN SLOGTEREN, E. (1955) Serological diagnosis of plant diseases. *Ann. appl. Biol. 42:* 122–8.

VAN SLOGTEREN, E. (1958) Ratelvirus als oorzaak van ziekten in bloembolgewassen en de mogelijkheden de infectie door middel van grondontsmetting te bestrijden. *T. PlZiekten. 64:* 452–62.

VAN SLOGTEREN, E. and M. P. DE BRUYN OUBOTER (1946) Investigations on virus diseases of Narcissus. *Daffodil and Tulip Year Book 12:* 3–20.

VAN SLOGTEREN, D. H. M. and C. J. ASJES (1969) Virus diseases in tulips. *Daffodil and Tulip Year Book 35:* 85–97.