

Invasion, dispersal and ecology of the South African neophyte *Senecio inaequidens* in The Netherlands: from wool alien to railway and road alien

W. H. O. ERNST

Department of Ecology and Ecotoxicology, Faculty of Biology, Vrije Universiteit,
De Boelelaan 1087, 1081 HV Amsterdam, The Netherlands

SUMMARY

Senecio inaequidens, a perennial pioneer plant, invaded The Netherlands at Tilburg with sheep's wool from South Africa in 1939, where it failed to establish a permanent population. In 1942 a new invasion from an expanding invader population at Liège occurred at Eijsden, establishing a new dispersal centre in southern Limburg, The Netherlands. In the 1980s a further dispersal throughout The Netherlands resulted in additional dispersal centres at the railway stations at Amsterdam and Hengelo. The dispersal along new railway lines in the Amsterdam region confirmed the importance of trains for occasional long-distance dispersal events because in general the majority of the anemochorous achenes remained in the vicinity of the parent plants. Expansion dynamics and ecology was studied in a new established population at the railway station in Hoofddorp. The species has a high self-fertility. Adaptation to the Atlantic climate of The Netherlands was accompanied by the selection for flowering earliness from August to May and prolongation of the flowering period to end of December. Achene mass mostly declined from high values in July to 70% lower ones in December. Low dormancy of early summer achenes allowed establishment of a new generation in the same year; late autumn achenes had a high dormancy and germinated in next spring. Dormant achenes persisted for two winter periods and survived frost at -15°C . Caterpillars of *Tyria jacobaeae* were recorded as leaf herbivores on *S. inaequidens*, but had nearly no impact on a plant's performance. The extinction or survival of the various founder populations as wool aliens in Europe is discussed in relation to founder effects, adaptation to winter temperature in western Europe, prolongation of the flowering period and the importance of modern traffic means and climatic changes for its rapid expansion after 1985.

Key-words: dispersal, dormancy, flowering, frost, germination, *Tyria jacobaeae*.

INTRODUCTION

Invasion is a natural process which governs the development of vegetation and ecosystems on continents on a scale of centennia or even millennia, as demonstrated

by the succession of dominant trees in Europe and North America after the last ice-age. Anthropogenic introduction of plant species across continents of the same hemisphere and across hemispheres are characterized by rapid transport over great distances, often simultaneously at various sites. Such a rapid introduction to a new environment may have major ecological and evolutionary consequences (Drake *et al.* 1989). *Senecio inaequidens* (Asteraceae), a perennial plant originally growing in Transvaal and Natal (South Africa) (Jäger 1988), has unintentionally been introduced with sheep's wool into several sites in Europe from 1889 onwards. The first occurrences in Europe were recorded in the vicinity of wool-processing factories near Hannover (D) in 1889 (Brennenstuhl 1995) and at Bremen (D) in 1896 (Kuhbier 1977). All other primary invasion sites are also related to wool industry: Edinburgh (1928) in Scotland (Lousley 1961), Liège (1922) in Belgium (Mosseray 1936), Mettmann (1922) and Leipzig (1938) in Germany (Stieglitz 1977; Kuhbier 1977) and Tilburg (1939) in The Netherlands (Adema & Mennema 1978). After several decades of a wool alien (Lousley 1961) and its restriction to the vicinity of the invaded sites, *S. inaequidens* started from 1950 onwards to expand throughout western, central and southern Europe, and to other environments than the surroundings of a wool industry.

Joenje (1987) postulated that rapid dispersal of neophytes will depend on their migration potential by means of modern traffic. The recent dispersal pattern of *S. inaequidens* partly supports this opinion, as shown by the preferential migration along railways (Koster 1991; Mazomeit 1991; Brandes 1993; Büscher & Loos 1993), motorways and suburban roads (Kehren 1995), and after transport with debris to ruderal sites (Tammaro & Giglio 1994). Recently it has started to extend its area along motorways from Atlantic and subAtlantic Europe to subcontinental East Germany (Griese 1996) and Kattowice in Poland (Ernst 1997, unpublished). Migration along river banks such as those of the Meuse from Liege into and within The Netherlands (Van Ooststroom & Reichgelt 1958; Van der Meijden *et al.* 1994) and into woodland clearings (Van der Meijden *et al.* 1994) also indicates the potential of non-anthropogenic long-distance dispersal. The invasion of the browncoal tailings between Aachen and Cologne and the further dispersal in the Cologne region may be by wind (Werner *et al.* 1991) or by human activities.

The ecology of the species, however, has received only little attention. It has been suggested that cold winters with very low temperatures and cool-wet summers may affect the persistence of this invader despite its potential for rapid reproduction (Werner *et al.* 1991). Most information is known from the plant/herbivore interaction. Four alkaloids have been identified in *S. inaequidens*; the high proportion of retrorsine in this alkaloid mixture let it differ from co-occurring *Senecio* species, *S. jacobaea* and *S. sylvaticus* (Bicchi *et al.* 1989; Witte *et al.* 1990).

The objective of this study was an evaluation of the impact of trains on the dispersal of the species and of the reproductive behaviour under controlled and field conditions in relation to its rapid expansion. I want to substantiate the hypotheses that (1) railways facilitate the establishment of new dispersal centres, (2) the prolongation of the flowering period (Adema & Mennema 1978), as a result of adaptation of the flowering cycle from the Southern to the Northern Hemispheric climate and of a sequence of warm summers in The Netherlands (global climatic change), has favoured achene production and expansion potential, (3) earliness of flowering will positively affect achene mass with increasing daylength (the reverse of the hypothesis of late flowering [Cavers and Steel

1984]), and (4) early flowering combined with increasing achene mass will shorten the reproductive cycle.

STUDY AREA

The occurrence of *Senecio inaequidens* was monitored throughout The Netherlands from 1983 to 1997 for the analysis of the importance of new dispersal centres of *S. inaequidens* along railways. Each year in October the presence of flowering plants near railway stations was registered by travelling along all main lines in The Netherlands. For the elaboration of the development of the distribution pattern additional information was taken from the specimens of the collection at the Rijksherbarium at Leiden and from published records.

The importance of the construction of new railways for the dispersal of this neophyte in relation to secondary dispersal centres was investigated in the Amsterdam region.

The main study area for population dynamics and ecology was the population at Hoofddorp station with its first establishment in 1989. Four sites were selected for detailed studies: site (A) was the founder site at the south-western end of the station building; site (B) was a steep, southerly exposed grassland on the railway embankment at the station, important for the plant/caterpillar interaction due to co-occurrence of *Senecio jacobaea*; site (C) a car park area at the border of the western railway embankment; site (D) a main road parallel to the railway at 100–150 m distance; site (E) is a cycle track north of road and separated by a 5–10 m broad, planted shrub girdle; site (F) is a new cycle track constructed in 1994 (see Fig. 2).

MATERIALS AND METHODS

Achene collection

Achenes of *Senecio inaequidens* DC were collected from 1991 onwards at identical sites in Hoofddorp, The Netherlands, as far as possible with monthly intervals and at the same sampling date each year so that daylength, but not solar energy, were identical among years. At each of the sites (C), (D) and (E) 10 plants were marked and used for sampling throughout a year and, if surviving, throughout all years. At each sampling date ripe achenes of 10 capitula, if present, were collected in paper bags and stored for 1 week at room temperature (20°C) prior to weighing on a microbalance (1 µg sensitivity, Mettler ME 30). At all sampling dates all remnant achenes from these and as many other plants as possible were collected for the other experiments. They were stored as long as necessary prior to experimentation at the above-mentioned room temperature. In addition achenes were collected at the railway stations of Amsterdam CS, Duivendrecht, Eijssden, Hoorn, Leeuwarden and Maastricht and abroad at the central railway stations of Duisburg and Mannheim in Germany (1991–94), a woodland clearing at Vielsalm in the Belgian Ardennes (1995), and at the Budel exit of the motorway Eindhoven–Roermond in The Netherlands (1995). Except for determination of the settling velocity of achenes the pappus was removed from the achenes prior to weighing and storage.

Development time of achenes

For the analysis of the development time of achenes, capitula with the outmost circle of flowers at the stage of receptive pistils were marked every 3 weeks, five capitula of

each of three selected, at least 2-year-old plants in 1995. From day 15 onwards, the marked capitula were controlled for achene maturity every day and capitula with ripe achenes removed. The number of marked capitula of plants in the climate chamber was reduced to five in each temperature regime. During flowering the visiting insects were only registered in 1995 and 1996.

Germination experiments

Sets of 100 achenes collected from July to December 1994 at the Hoofddorp sites (C), (D) and (E) were a day after harvest imbibed on moist filter paper in plastic boxes (55 × 55 × 25 mm). They were kept at a day/night temperature rhythm of 20°C/15°C (12/12 h) and a daily photon flux of 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (12-h light/12-h dark). Achenes affected by fungi and seedlings were removed after counting. Due to similar germination and survival rates the three sites were pooled to one harvest cohort.

At the start of the germination experiment in 1995 100 achenes of the Hoofddorp site (C) were laid on moist filter paper in the above-mentioned plastic boxes and exposed either to the above given conditions in the laboratory or to the ambient soil temperature in a grassland near the car park; for this purpose the plastic boxes were buried into the soil at 1 cm depth. The boxes were controlled each week or—if germination was slow—2–3 weeks. The experiments lasted as long as the last seedling emerged. Every 3 months the filter paper was replaced by a new one.

Dispersal and establishment

For the measurement of settling velocities achenes with pappi were collected as complete capitula and stored carefully in plastic boxes. After 1 day single achenes were removed from the capitulum and settling velocity was measured by dropping them down a plexiglas tube and timing their descent with a digital stopwatch. The perspex tubes had a diameter of 15 cm and were 1.50 m in length. Three replicate measurements of falling time were taken for each achene, 10 achenes collected in August, October and December 1992.

For analysing the dispersal distance of achenes three plants, pregrown at the climate chamber from February to April 1996, were planted close together in garden soil at Hoofddorp, 2 km away from the nearest *Senecio* site. All achenes were allowed to spread. In early November 1996 the three plants were removed, but the position of the main stem was marked by a nail as centre for the dispersal distance. From this time onwards the number of seedlings was recorded each week; the distance of seedlings to the former position of the parent plants was measured and afterwards the seedling removed. This experimental site was and will be monitored for several years.

To analyse the cause of the low invasion of *S. inaequidens* into lawns and grasslands near railway stations, achenes of the 1993 collection (July–October) having lost nearly all dormancy were sown in October 1994 on a lawn and a park grassland, both 400 m away from the railway station in an area without *S. inaequidens* (100 achenes per plot of 1 m², three plots per site). In three adjacent plots the grass cover was removed from three subplots of 25 × 25 cm⁻² at each site and once more 100 achenes from the 1993 collection were sown on bare soil of each subplot. In April 1995 in three adjacent subplots at each site 20 1-day-old seedlings were planted under the grass cover. Germination and development up to the flowering stage were recorded from autumn

of 1994 up to winter 1996. Flowering plants were removed to prevent the establishment of a new population.

Impact of temperature

From 1994 onwards, each spring the survival of established plants at the Hoofddorp sites and on the railway embankment at Duivendrecht was controlled by following the flushing of new leaves and shoots and the start of flowering.

To test the hypothesis of a positive effect of warm summers experimentally, seedlings were planted in a mixture of garden soil and dune sand (1:1, wt/wt) and grown in a climate chamber at an illumination period of 12/12 h (day/night) at a high temperature regime of 30°C/27°C (day/night) and at an illumination period of 18/6 h at a low temperature regime of 20°C/15°C and a photosynthetic flux density of 250 and 170 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in high and low temperature regimes, respectively, so that their irradiation was similar. After achene ripeness of the first capitula the high-temperature plants were transferred to the climate chamber with the daily 20/15°C cycle. Just after transfer all flowering and fruiting capitula were removed except the capitula in the early bud stage to prevent an effect of the former treatment.

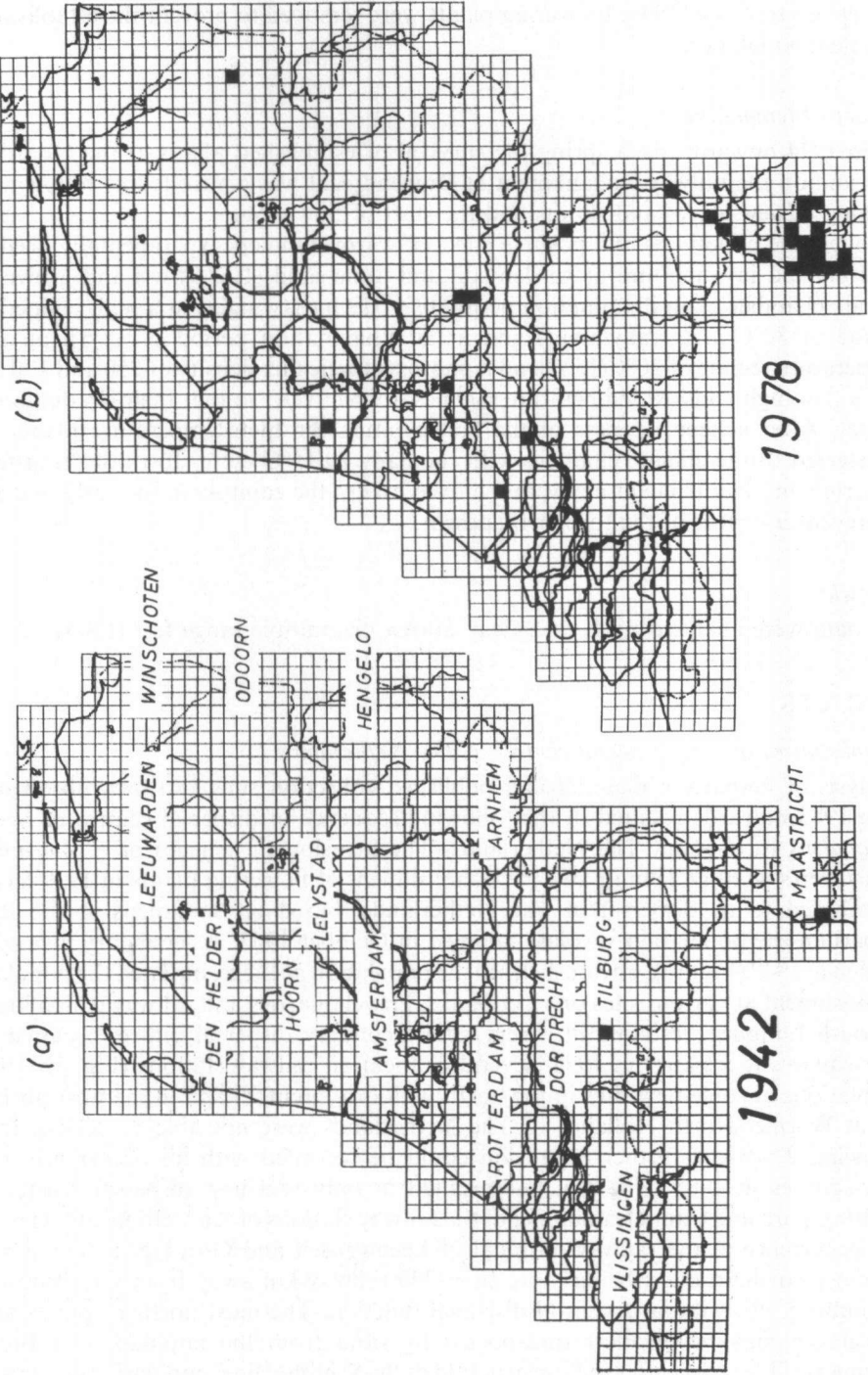
Statistics

The data were analysed by 1- or 2- way ANOVA or multiple range test (LSD).

RESULTS

Establishment of new dispersal centres in The Netherlands

Analysis of herbarium material and published collection sites and own observations from 1983 onwards resulted in the following sequence of dispersal centres of *Senecio inaequidens* throughout The Netherlands. The invasion of achenes of *S. inaequidens* with sheep's wool at Tilburg and the establishment of flowering plants in 1939 has not contributed to its dispersal in The Netherlands; based on specimens at the Rijks-herbarium the population was last sampled in October 1953. A secondary invasion at Eijsden in 1942 (Fig. 1a), obviously from the population at Liège, initiated the population establishment at various sites on river banks, gravel quarries and railway embankments in South Limburg, resulting in a very vital secondary dispersal centre, occupying 30 hour-squares ($5 \times 5 \text{ km}^2$) in 1978, several of them on railway stations (Fig. 1b). Small populations at some new sites in the north (Odoorn/Drenthe) and in the west (disposal site at Wormer/North Holland) of The Netherlands were not able to persist. In the following 8 years a further expansion could be recorded with an occurrence on 89 hour-squares in 1985 (Fig. 1c), but resulted in only two new dispersal centres, the shunting-park and train-cleaning site of the railway stations of Amsterdam and Hengelo. The occurrence at the railway terminal of Leeuwarden and Groningen were some of the most northern ones, being more than 200 railway-km away from the nearest site in Limburg, but without a central dispersal function. The most northern plants at the Eemshaven may be invaders transported by wind from the population at Bremen (Germany). Two years after the construction of the Schiphol line, populations established on the embankments at the Sloten junction of this line with the Hoofddorp–Amsterdam South line (5–7 km away from the Amsterdam population) and at Hoofddorp where the population dynamics of this population was studied in more detail. From 1993



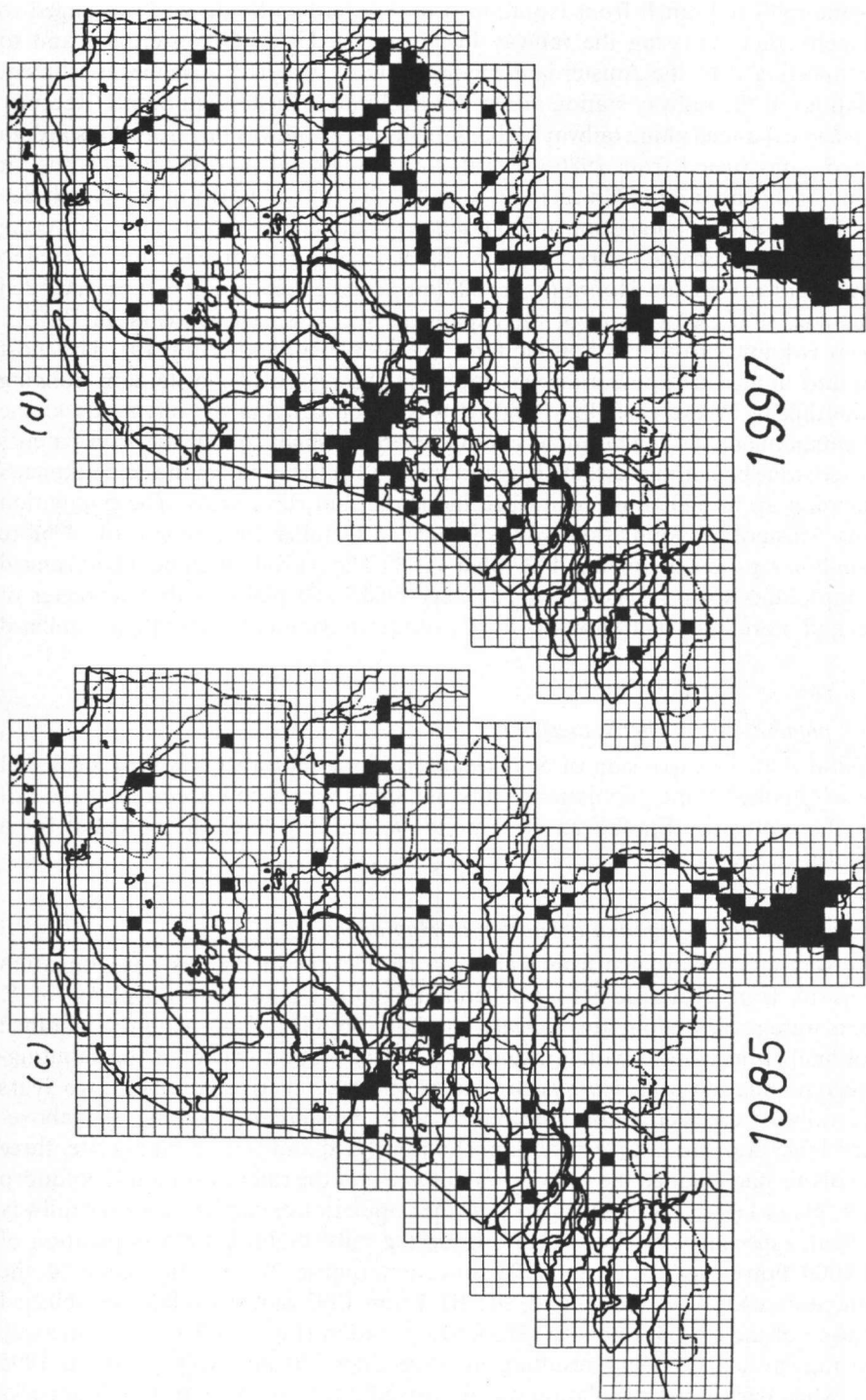


Fig. 1. Distribution of *Senecio inaequidens* throughout The Netherlands from 1939 to 1997. The sources of information for the four dispersal periods are the following: (a) herbarium collection; Mennema *et al.* (1985); (b) herbarium collection; Adema & Mennema (1978); (c) herbarium collection; Koster (1986); Mennema *et al.* (1985); (d) Duistermaat (1994); Koster 1991; Van der Meijden *et al.* (1994); own registration from 1983 onwards).

onwards the railway branch from Hoofddorp to Amsterdam South was prolonged to Duivendrecht, there crossing the railway line from the Utrecht–Amsterdam, and to Weesp connecting it to the Amsterdam–Hengelo line; it resulted in the establishment of populations at the railway station at Duivendrecht and Amsterdam South. Recently *S. inaequidens* expanded along railway embankments of the railway line from Amsterdam to Lelystad, constructed from 1986 onwards, into Flevoland (two individuals just at the railway bridge across the IJmeer) and into North Holland north of the North Sea Channel. The numerous population at Zaandijk may be a new dispersal centre; flowering individuals were still scarce further north at Koog ($n=5$), Krommenie ($n=2$), Heiloo ($n=3$), Alkmaar ($n=8$) and Hoorn ($n=c. 60$) and Anna Paulowna ($n=2$), as recorded on 11 October 1997. As a result of the expansion over the past 55 years, in 1997 *S. inaequidens* is known from 173 hour-squares in The Netherlands (Fig. 1d). The most extended and numerous population was found in the region of Amsterdam, ranging from Sloterdijk to Weesp (c. 17 km long). It was accompanying the outer side of the railway embankments as 1–2 m broad continuous borderline, colonizing open patches in the coarse stone beds and grassland between rails and at the slopes of the embankments and expanding up to 500 m into disturbed industrial and rural areas. The population size of the Amsterdam population was estimated in October 1997 to consist of more than 10 million reproducing plants, 1–27 plants m^{-2} . The reproduction per plant ranged from young plants with 3–7 flowers up to very bushy old plants with a diameter of 60–75 cm and more than 1000 capitula, finally producing annually more than a milliard achenes.

Motorway populations in The Netherlands

It was found that the expansion of *S. inaequidens* along motorways is very local. If I have not overlooked some populations, only one huge population occurred at the exit Budel of the motorway Eindhoven–Roermond, which may have the potential for a new dispersal centre.

Invasion sequence and population expansion at Hoofddorp

A new railway was constructed from Leiden to Hoofddorp in 1981 as a prolongation of the railway from Rotterdam to Amsterdam South. Up to 1987 no plants of *S. inaequidens* were present along this railway line. In 1986 this railway acquired a branch (Schiphol line) connecting it with Amsterdam Central Station, where at the shunting-yard a huge population of *S. inaequidens* had established (cf. Koster 1986). Two years after the railway connection of Hoofddorp with Amsterdam, passing the above-mentioned huge population at Amsterdam shunting-yard and train cleaning site, three flowering plants had invaded the railway embankment at the railway station Hoofddorp in 1989, i.e. phase 1 (Fig. 2, site A). Up to 1992 the population expanded along the railway embankment, especially growing 1–2 m outside the rails, building up a population of at least 1000 flowering plants in a SW direction (phase 2), and the slope of the embankment in a SE direction (Fig. 2, site B). From 1992 onwards plants established at the margin of the car park next the Hoofddorp station (Fig. 2, site C), 3–55 m away from the railway embankment resulting in more than 330 flowering plants in 1995 (phase 3), when part of the population was destroyed due to road reconstruction works and moving of the car park to the SE site of the station; at non-affected areas around 120 flowering plants were recorded in September 1997; four of them belonged to the

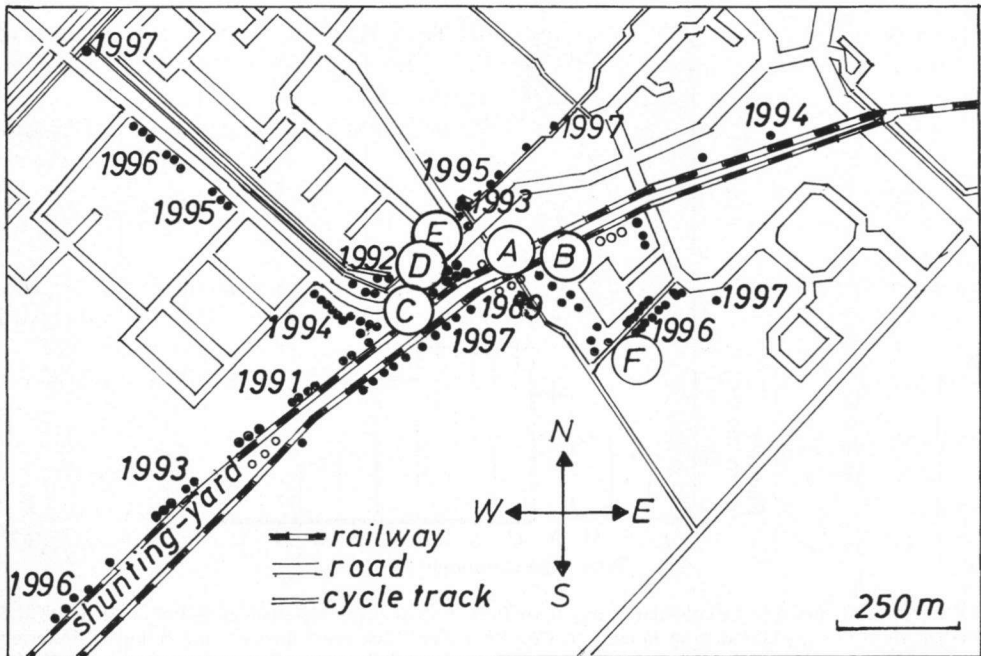


Fig. 2. Chronosequence of the local expansion of *Senecio inaequidens* in the vicinity of the railway station at Hoofddorp. The indicated sites are: (A) the founder population at the railway station in 1989 ($n=3$), (B) railway embankment near the station, (C) car park, (D) road site, (E) cycle path at that road site, (F) new cycle path.

individuals marked in 1992. From 1992 to 1996 more than 200 flowering plants established along the road site (Fig. 2, site D) opposite to the railway station at some small bridges, and 16 plants at a lawn margin of an accompanying (old) cycle-track (Fig. 2, site E). This lawn was mown twice every year in June and August, decapitating the upper shoots. At the start of reconstruction and expansion of the railway from 1995 onwards, several hundred plants in a grassland with co-occurring *S. jacobaea* and on the southern part of Hoofddorp shunting-yard were eliminated (phase 4). However, at the same time the population expanded in a south-westerly direction along the railway to Leiden, more than 1500 flowering plants in 1996, and in southerly direction along a new car park and a new cycle-track, 100–150 m south of the railway embankment with nearly 280 flowering plants in 1997. A further expansion of the population was recorded in 1997 (phase 5): 780 m along the old cycle-track in a northern direction with 17 plants flowering the first time in that year; many open patches in the west-exposed lawn of the broadened and reconstructed road were colonized after summer 1996, *c.* 400 plants flowered a year later. In 1997 two plants were flowering and reproducing near a traffic light, 1 km away from the original site of introduction in NW direction. Despite much disturbance (soil removal, road and railway construction) the population expanded from three plants in 1989 to around 2500 or more reproducing plants in 1997. The number of capitula per plant ranged from a mean of 26 ± 5 capitula in small plants ($n=50$) and 230 ± 45 capitula ($n=50$) in tall, at least more than 2-year-old plants. In 1997 one of the 5-year-old plants had produced 487 capitula with ripe achenes up to 5 October 1997 and supported 67 flowering and ripening capitula and 231 capitula

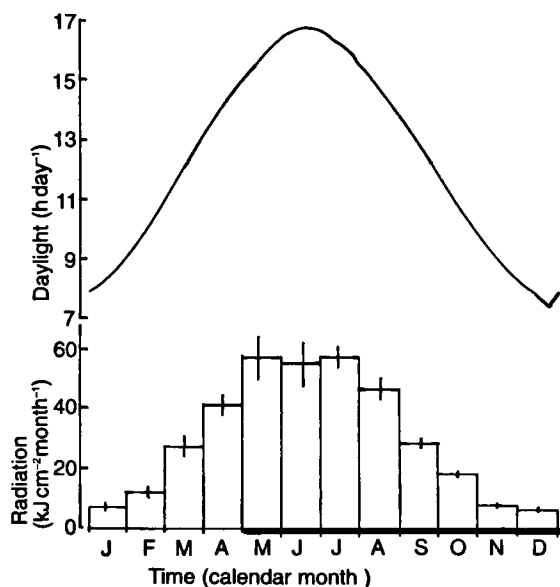


Fig. 3. Monthly mean (\pm SE) of solar energy from 1991 to 1996 at the Metereological Station Schiphol and the length of the day period from January to December. The black beam indicates the period of flowering of *Senecio inaequidens* in the Amsterdam region from 1986 to 1997.

in the bud stage. With 50–80 fertile achenes per capitulum the annual reproduction of the Hoofddorp population will amount to more than 20 million achenes in 1997.

Flowering time

A change of the hemisphere may affect the flowering period of the invader. All specimens of the invaders at the Tilburg site collected between 3 August 1939 and 26 October 1953 had flowers. The first specimen with flowers in July was from 24 July 1978 at the railway station Beek-Elsloo (Limburg). Adema & Mennema (1978) gave, in the determination table, the period from August to October as flowering period, but added in the text that in the meantime it was also flowering from June to July and from November to December. In 1992 a few individuals of *S. inaequidens* in the Amsterdam region started flowering on 14 May; after the mild winter of 1993/94 the first flowering capitulum was recorded on 3 May 1994, although most of the individuals from the populations at Amsterdam and Hoofddorp started flowering in late June. Thus flowering started when the daylength was above 15.1 h and flowering finished in mild winters (1993 and 1994) at a daylength of only 7.4 h (Fig. 3). At the start of the flowering period only a few capitula opened per day, independent of the daily solar energy, varying from 0.5 kJ cm⁻² d⁻¹ on cloudy days to 2.94 kJ cm⁻² d⁻¹ on very sunny days. Throughout the years there were two main flowering periods, one from mid-July to mid-August and one from mid-September to mid-October. From mid-November onwards the number of flowering capitula was very small, often not surpassing 15 capitula per census day at all Hoofddorp sites together.

Table 1. Impact of the season on achene mass (μg) of *Senecio inaequidens* (mean \pm SE) at the same site (Hoofddorp, railway station). $n=30$ achenes, weighed at random from a bulk collection of five capitula of each of 10 plants per sampling date. Data with different superscript letters per column are significantly different at least at $P<0.05$. NA=no achenes were available

Date of achene sampling	Year of collection				
	1992	1993	1994	1995	1996
15 July	NA	289 \pm 49 ^a	344 \pm 28 ^a	272 \pm 74 ^a	NA
28 August	291 \pm 56 ^a	301 \pm 48 ^a	259 \pm 32 ^b	312 \pm 39 ^a	235 \pm 28 ^a
24 September	262 \pm 34 ^b	254 \pm 33 ^b	237 \pm 27 ^b	240 \pm 34 ^b	229 \pm 32 ^a
15 October	223 \pm 256 ^{bc}	210 \pm 47 ^c	240 \pm 32 ^b	270 \pm 65 ^{ab}	252 \pm 43 ^a
15 November	NA	195 \pm 36 ^{cd}	234 \pm 40 ^b	228 \pm 34 ^{bc}	240 \pm 17 ^a
2 December	189 \pm 19 ^c	180 \pm 33 ^d	237 \pm 32 ^b	205 \pm 34 ^c	234 \pm 43 ^a
31 December	250 \pm 52 ^b	NA	NA	NA	278 \pm 23 ^b

Achene development and achene mass

Although the female flower stage within one capitulum lasted on average 3 days, all achenes of a capitulum matured on the same day. The time of achene development, i.e. from fertilization to achene release, decreased from 23.5 ± 0.1 day for the first achenes in early July to 17.1 ± 0.2 day from mid-July to late September and then rapidly increased to 34.8 ± 3.7 day in November and December. Flowers that were naturally and/or hand-fertilized from late November onwards did not produce viable achenes (mass $<80 \mu\text{g}$ per achene without pappus). The achene filling decreased from a summer mean of 91 to 26% during late autumn and winter.

The mass of the achenes (without pappus) changed during the reproductive season and varied at the same collection date among years (Table 1), but not between sites. Earliness of flowering resulted in a high achene mass from July to August; then the achene mass remained constant (1994, 1996) or declined up to the early December. The highest achene mass in July 1994 was nearly double that in December 1993. This general pattern had two exceptions: in 1992 and 1996, when viable achenes could be harvested on 31 December, the achene mass was either the highest of the whole reproductive season (1996) or similar to that of September 1992.

Achene mass collected at other sites were in the same range, but achenes on the railway from Duisburg to Mannheim ripened mostly 1–2 weeks earlier than at the sites in Hoofddorp and Amsterdam. Achenes collected at the Central Station at Duisburg/D on 27 August 1992 had a mass of $246 \pm 49 \mu\text{g}$ ($n=30$) being very similar to that from 18 July 1997 ($230 \pm 24 \mu\text{g}$, $n=30$), the latter being comparable to the $235 \pm 28 \mu\text{g}$ collected at Hoofddorp on 28 August 1997; at this latter site no ripe achenes could be harvested on 17 July 1997. Achenes from plants on a woodland clearing at Vielsalm/B on 1 August 1995 had a mass of $275 \pm 18 \mu\text{g}$, similar to the high achene mass in that year at Hoofddorp. Achene mass of all the other sampling sites did not differ from the mass of achenes collected in the same period and year at Hoofddorp.

Plants grown in a climate chamber at a temperature regime of 20/15°C and 30/27°C (day/night) opened after 79 days, the first flowers independent of the temperature regime. Achenes matured after a further 17 days, thus resulting in a minimum time of 96 days for one reproductive cycle. The achenes of both treatments, however, differed

Table 2. Achene mass (μg) of *Senecio inaequidens* (four plants per treatment) grown in a climate chamber at a temperature of 20/15°C and 30/27°C (day/night), the latter also after a transfer to the low temperature regime. Different superscript letters indicate significant differences at $P < 0.001$

Temperature regime	Number of achenes	Mean achene mass \pm SE
20/15°C	75	307 \pm 34 ^a
30/27°C	69	282 \pm 28 ^b
30/27°C to 20/15°C	77	370 \pm 55 ^c

in mass (Table 2), being 9% ($P < 0.001$) higher at the low temperature regime (20/15°C). Transfer of the plants from 30/27°C to 20/15°C increased the mass of the achenes by 30% without changing time to achene maturity.

Winter temperature and plant survival

Frost of -5°C for one or two nights stopped the initiation and development of new capitula. It did not affect achene production, but reduced the number of filled achenes. As a perennial plant *S. inaequidens* can hibernate with viable roots and dormant buds near the base of the shoot, in mild winters such as those of 1993/4, 1994/5 and 1995/6. The various frost periods of the winter 1995/6 (from 26 December 1995 to 31 March 1996) with a minimum temperature of not less than -8°C did not affect the seedlings having four to eight green leaves. The strong winter 1996/7 caused the death of seven of 73 and six of 41 established plants at Hoofddorp and Duivendrecht, respectively; none of the seedlings ($n = 138$) survived. The dead plants were found on microsites exposed to easterly winds; they did not develop new leaves and shoots in spring 1997. In contrast, wind-protected plants survived. In that year plants at very open patches at Duivendrecht, however, delayed the development of new shoots by nearly a month and flowering by nearly 5 weeks in comparison to the protected plants at Hoofddorp, already flowering in late May and reproducing in July. The many seedlings at the various field sites in April 1997 indicated that achenes were not injured by frost below -15°C . Achenes kept in plastic boxes near the soil surface were frozen during the winter 1996/97, but survived exposure to night temperatures between -10°C and -15°C and a period of 16 permanent frost days.

Germination

Each monthly cohort had its own germination pattern which fits with the general environmental conditions at achene maturity. The July cohort had a high primary dormancy (Table 3) which was slowly released the first month after achene ripeness (1–2% germination), but decreased strongly after 3 months when the germination percentage of $50 \pm 3\%$ was realized. The dormancy period of the August cohort lasted only 1 month; after 2 months 65% was germinated. A similar pattern was found for the September cohort. The dormancy of the cohorts of October, November and December was very high and was only fully broken after 270 to 330 days.

Achenes which were exposed in plastic boxes *in situ* to the ambient temperature conditions from August 1995 onwards gave very different results from that under

Table 3. Germination (mean \pm SE) of the monthly cohorts of *Senecio inaequidens* when the achenes were imbibed immediately after harvest in 1994 and exposed to a day/night temperature regime of 20/15°C. The underlined values indicate the potential for germination in late summer and early autumn, the italic values indicate the potential for germination in spring

Days after imbibition	Cohort of the month					
	July	August	September	October	November	December
30	4 \pm 2	25 \pm 7	30 \pm 8	10 \pm 0	1 \pm 1	6 \pm 2
60	14 \pm 6	<u>65 \pm 3</u>	<u>53 \pm 11</u>	12 \pm 2	4 \pm 2	10 \pm 1
90	<u>50 \pm 2</u>	87 \pm 3	56 \pm 10	13 \pm 1	6 \pm 2	<i>30 \pm 1</i>
120	59 \pm 1	89 \pm 3	59 \pm 7	13 \pm 1	35 \pm 9	30 \pm 1
150	61 \pm 1	92 \pm 4	61 \pm 7	13 \pm 1	36 \pm 9	32 \pm 1
180	67 \pm 3	93 \pm 5	67 \pm 5	22 \pm 2	37 \pm 7	32 \pm 1
210	81 \pm 1	—	68 \pm 6	<u>45 \pm 1</u>	38 \pm 8	32 \pm 1
240	<i>95 \pm 1</i>	—	79 \pm 9	53 \pm 3	40 \pm 10	63 \pm 7
270	96 \pm 2	—	80 \pm 10	63 \pm 2	<u>45 \pm 9</u>	<u>88 \pm 1</u>
300	—	—	—	67 \pm 3	46 \pm 9	—
330	—	—	—	70 \pm 2	47 \pm 8	—
365	—	—	—	71 \pm 2	49 \pm 10	—

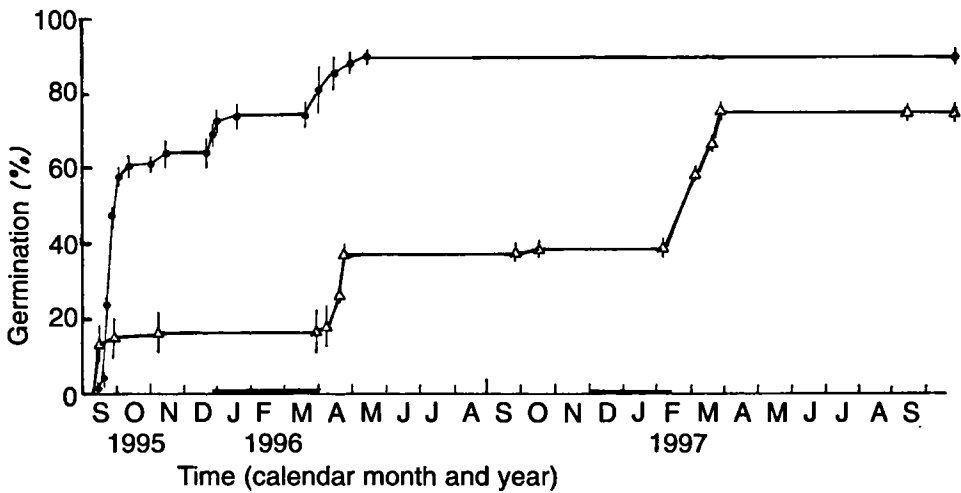


Fig. 4. Mean germination (three replicates of each 100 achenes) of the September achene cohort of *Senecio inaequidens*, harvested in September 1995 and immediately exposed to ambient temperatures at soil level in Hoofddorp (triangles) or to a day/night temperature regime of 20/15°C in the laboratory (filled circles). The non-germinated achenes contained no viable embryo at the end of the experiment. The black beam indicates the frost period with frozen achenes in the field.

laboratory conditions. The achenes of the summer cohorts germinated more rapidly under the warmer field conditions than under laboratory conditions, but stopped germination after 3 weeks (July cohort), after 2 weeks (August cohort) or even after a few days (September cohort, Fig. 4); they remained dormant up to April of the next year. Achenes exposed in October and November to ambient field temperature did not germinate at all up to April of the next year, when the achene cohort from October

Table 4. Dispersal distance (m) of achenes of *Senecio inaequidens* from the parent plants in an experiment on bare soil, as analysed by the appearance of seedlings. The three parent plants were removed in November 1996

Distance to parent plant (m) Appearance of seedlings (month)	0-1	1-2	2-3	3-5	5-10	>10
September/October 1996	27	0	0	0	0	0
April 1997	316	2	1	0	0	0
September 1997	119	4	3	1	0	0
1-10 October 1997	38	7	3	1	1	0

and November germinated within 1 month. Then water, together with the remnant achenes in the boxes, was frozen from 26 December 1995 to 31 March 1996, when germination started on 4 April 1996 for 1 month. After a further dormancy period only a few achenes germinated in September and October 1996, varying among cohorts 1-10%. A new frost period from December 1996 to early February 1997 stopped germination which restarted on 16 February and lasted to mid April. All non-germinated achenes had ceased in September 1997.

Dispersal and establishment

The mean settling velocity of achenes in calm atmosphere was $0.32 \pm 0.07 \text{ m s}^{-1}$, but was strongly dependent on achene mass: $0.28 \pm 0.07 \text{ m s}^{-1}$ for achenes weighing $208 \pm 40 \mu\text{g}$, $0.41 \pm 0.04 \text{ m s}^{-1}$ for achenes with a mass of $273 \pm 13 \mu\text{g}$. The three plants in the dispersal experiment produced 288, 319 and 322 capitula at 12-63 cm above soil level. With a mean of 79 ± 10 filled capitula ($n=35$) in other plants at Hoofddorp in the same year, the number of dispersed achenes from the experimental plants was calculated to range between 18 000 and 29 000. Only 27 seedlings were recorded in autumn 1996, all within 0.5 m and 1.0 m distance from the parent plants. In April 1997 a further group of 316 seedlings established within 1 m, two within 2 m and one within 3 m from the parent plants. The next seedling cohort appeared from September 1997 onwards; most of the seedlings were once more recorded in the range from 0.2 to 1 m, but a few seedlings in a distance of 1-4 m (Table 4). Only one seedling was found 7.6 m away from the former parent plants.

Achenes sown in October 1994 in the grass layer of the lawn and a grassland did not deliver any seedlings in the next spring and autumn. Seedlings planted in April 1995 underneath the grass layer grew slowly, but all died off during the first dry period in July. From achenes sown in October 1995 on bare soil of the lawn and grassland, seedlings were recorded in April 1996; they flowered late August 1995. In October the mean mass of these plants was $3.3 \pm 0.8 \text{ g}$, having on average six mature capitula, 19 flowering capitula and 35 capitula in the immature stage.

Plant-animal interactions

Flowers of *S. inaequidens* were regularly visited for pollen consumption by the hoverflies (Syrphidae) *Episyrphus balteatus*, *Eristalis arbustorum*, *E. tenax*, *Metasyrphus latifasciatus*, *Sphaerophoria scripta* and *Syrphus ribesii*, for nectar by the butterflies *Lasiomata megera* and *Coenonympha pamphilus*, and for both sources by the solitary

hymenopteran *Halictus* sp. From October onwards both *Eristalis* species frequently visited the flowers of *S. inaequidens* because it was one of the few plant species flowering at that time. Pollen feeding activity of the hoverflies lasted from 1–2 s by *S. scripta* up to 12 s by *E. tenax*. The bumblebee *Bombus pratorum* was only incidentally observed on flowers.

Despite a well-developed population of *S. jacobaea* in the neighbourhood of *S. inaequidens*, eggs of *Tyria jacobaeae* were deposited on the neophyte at Hoofddorp site (B, Fig. 2). Caterpillars fed freely on the leaves and developed to maturity. This is the first record of *T. jacobaeae* on the neophyte, thus once more questioning (Rothschild *et al.* 1979) the monophagy of *T. jacobaeae* on *S. jacobaea* (Soldaat 1991, Van der Meijden 1979).

DISCUSSION

Adaptation to the European atlantic climate

Which characteristics of plants from South Africa invading Europe have to be changed to adapt to the atlantic climate? At its original habitats in South Africa *Senecio inaequidens* grows in sandy gritty river banks of periodically, and rocky sites of permanently flowing rivers in Natal and stony grassland on hill slopes in Transvaal and Natal between 1400 m and 2850 m above sea level (Hilliard 1977). Industrial areas in Europe are therefore not an uncommon ecological site for such a species from stony environments. However, the invader has to adapt to the change of the growing season from August to April in South Africa to April until October in The Netherlands, to an Atlantic climate with cold and wet winters instead of cool and dry winters in South Africa, and to lower mean winter temperatures and longer frost periods, whereas the summers may be cooler in the Atlantic climate. The extinction of many of the wool alien populations in Europe may be caused by a too-small number of invading and released achenes, and insufficient adaptation(s) to the Atlantic or cold-continental climate. The population at Tilburg (NL), obviously remaining small, survived from 1939 to 1953 (based on herbarium specimens); the populations at Leipzig (D), Hannover (D) and Mettmann (D) disappeared within a few years, all prior to 1945. The disappearance of some new founder populations in The Netherlands may be also due to a too-small population size, or due to changes of the environmental conditions, e.g. vegetation succession on woodland clearings.

How has the invader adapted its flowering period to the growing season of the Northern Hemisphere? The recorded flowering from August to October in the period from 1939 to 1977 is in agreement with the early flowering time in South Africa, even if the collection date from the herbarium specimens may be biased by the preference of a collector. Therefore, after invasion only a little plasticity in the timing of the flowering was necessary to reproduce in the Atlantic climate of Europe. The extension of the flowering period to December from 1977 onwards fits with the main flowering time in South Africa, but the cooler winter temperature may demand an adaptation of the development temperature of achenes. The deleterious effect of a frost of -5°C on capitula development indicates that the adaptation process has not resulted in a frost resistance of capitula. The length of the adaptation to low temperature can be estimated to be 55 years, from the invasion in 1922 at Liège up to December flowering in 1977.

The selection for earliness in flowering is still in progress. In The Netherlands the

flowering period is prolonged by adjusting the start of flowering from August in 1940 to June in the 1970s and recently to May in the 1990s. A similar acceleration of the flowering time from June to early May was reported from plants in the vicinity of Cologne (Moll 1989). The selection for earliness is obviously a very time-consuming process, more than 65 years; this is twice the time for selection of early flowering in the summer annual *Rhinanthus angustifolius* in early mown grassland (Ter Borg 1985). A long flowering period makes *S. inaequidens* similar to many species of disturbed habitats. The occurrence of two flowering peaks on the same plant may also indicate another, not-yet-finalized adaptation process, i.e. optimalization of flowering; the inheritance of this characteristic involves many genes, as shown in the annual weed *Capsella bursa-pastoris* (Hurka *et al.* 1976). A selection for an early start of flowering may affect achene mass and stimulate dormancy polymorphism. This study confirms the variation in seed (achene) mass produced by individuals in other plant species (Cavers & Steel 1984). It contradicts the suggestion by Harper *et al.* (1970) that plants with indeterminate growth forms such as *S. inaequidens* should have a low variation in seed mass. The general decline of achene mass with shortening of the daylight period may be related to the availability of carbohydrates for achene filling and a lack of internal regulation of the number of achenes per capitulum. Indeed, the high achene mass in the late-December collections (Table 1) was related to a few fertile capitula with 17 ± 3 filled achenes per capitulum. However, the stability of the achene mass during the August to November period of 1996 cannot (yet) be explained. It demonstrates only that the plasticity in this character, although referred to as widespread (Silvertown 1989), demands a comparison of the same individual over years because it may be the result of different processes.

Indeed *S. inaequidens* has a high degree of dormancy polymorphism of the achenes which will be imposed by external factors because the same individual can produce achenes with very different degrees of dormancy. Achenes with the highest mass, i.e. those of July to September, had a monthly cohort-specific dormancy pattern. The short dormancy of the several achenes of the July cohort, lasting only a few days (Table 3), can give a new generation of achenes in the same year, as suggested by Werner *et al.* (1991) for achenes germinating in the vicinity of Cologne from July to August. Germination in July will demand wet and warm weather during summer. The postulated development time of 90 days between germination and flowering has been substantiated by the experiments in the climate chamber; plants flowered after 79 days at high radiation flux (Table 2). The few seedlings emerging in July or August can indeed result from achenes produced by early summer flowers. Therefore it is likely for plants growing at very sunny sites that a full life cycle is finalized in the same year. The high germination rates of the July and August cohorts in October fit well with the chance of optimal germination conditions in late September and early October in the Atlantic climate of Europe, but it will be not feasible in the dry winter of South Africa. Autumn germination is obviously one of the adaptations of the invader, being comparable with many winter annuals which germinate during October and early November (Ernst 1981, Rozijn & Van Andel 1985), but this seedling cohort of the invader demands a further adaptation to survive at low winter temperatures; the high mortality of seedlings during the strong frost period of the winter 1996/7 is an indication of an insufficient frost resistance in contrast to the surviving winter annuals. Achenes maturing from October to December have a high depth of initial dormancy and a certain degree of frost resistance; both will be a conservative characteristic of the invader which also fits also the European

winter. In the higher altitude range of its occurrence in South Africa, the Highveld and the afromontane region in Natal, minimum winter temperatures are just below -10°C whereas at lower altitudes it is just below zero. However, a special trait for the Atlantic winter, i.e. dormancy at external high water supply, has to be selected in dormant achenes and was indeed realized, as shown by the survival of imbibed, frozen achenes (Fig. 4).

Other environmental factors (Jäger 1988) such as global climatic change, i.e. long and warm summers and the mild winters of the past 20–30 years in western Europe, may have facilitated the survival of established plants. The evolution of earliness of flowering will profit from a warm and early spring because the flower initiation is independent of daylength and vernalization. Such favoured mature plants produce manyfold more achenes already early in the season than juvenile ones and magnify the achene production. The sensitivity of established plants to strong frost and/or long winter periods, as experienced in the winter 1996/7, indicate the advantage of climatic warming and can explain its slow expansion into continental Europe. The recent dispersal throughout Southern Africa may be a further support of the global climatic change impact on this invader from South Africa.

Adaptation for population expansion

Which adaptations are necessary for a population explosion? Jäger (1988) has suggested some population-internal factors and some external factors which may explain such a sudden change in population behaviour of neophytes: introduction of new ecotypes, genetic changes in the population (founder effect), surpassing a critical population level, anthropogenic changes of environmental factors and change in local or global climate.

Jäger's (1988) suggestion of an introduction of new, more expansive ecotypes can nearly be excluded for *S. inaequidens* in western and central Europe because only a few old invasion sites (Liège, Bremen, Verona) (Werner *et al.* 1991) have developed into dispersal centres.

With regard to the founder effect (Hedrick 1984) it is very likely that only a few achenes have been released from sheep's wool at industrial sites. Therefore each population at the various European sites has obviously started from a few individuals. Such a founder effect will cause chance changes in allelic frequencies which can undergo large fluctuations in different generations in an unpredictable pattern. The success of an invader will be very dependent on the adaptation of its parents. The high self-fertility of *S. inaequidens* which it has in common with other *Senecio* species (Comes & Kaldereit 1996) may restrict the success of a population if the genotypes are not well adapted to the new environment or enhance its development in the case of highly adjusted genotypes. The visit of flowers of *S. inaequidens* by hoverflies, solitary bees, bumblebees and butterflies may contribute only a little to the gene flow within small local populations. Therefore it is conceivable that the long lag-phase between invasion and population expansion lasting 20–50 generations is an indication of not sufficiently adequate genotypes at arrival in the new environment. Such a long lag-phase is not uncommon in neophytic plant species arriving from other continents in Europe (Jäger 1988).

As soon as a population has surpassed a critical size the anemochorous achenes will have a greater chance to depart far enough from the parent site, although most dispersal units, also anemochorous ones of other species, were found less than 1.5 m from the parent plants (De Jong & Klinkhamer 1985). The settling velocity of the achenes of

0.32 m s^{-1} in windstill atmosphere is in the range of other anemochorous fruits (Bostock 1978; Andersen 1992; Ernst & Kessler 1995) and indicates a good potential for anemochory. The establishment of *S. inaequidens* on woodland clearings, being far away from railways and motorways, are evidence of wind transport. The first establishment on a clearing in The Netherlands is that near Odoorn in Drenthe (herbarium specimen from 1978). The origin of the achenes may be from a population in Limburg (c. 250 km travel distance by south-westerly winds) or near Bremen (c. 130 km by north-easterly winds). Although *S. inaequidens* is growing on very open sites, enabling good thermic conditions in summer and early autumn, the scarce occurrence on woodland clearings in The Netherlands, Germany (Büscher & Loos 1993) and Belgium (Ernst, unpublished observation) allows doubt of the efficiency of anemochory for long-distance transport. Many, if not all, populations of *S. inaequidens* in The Netherlands may be derived from founder plant(s) which invaded as wool alien at Liège (Mosseray 1936). The failure of a local dispersal of the invader at the Tilburg site is an argument against its involvement in the establishment of the Eijsden population. It lasted two decennia (1922–42) to bridge a distance of 16–20 km from Liège (Belgium) to Eijsden (The Netherlands) along the river banks by air or in the water of the Meuse. Transport by wind is also discussed for its establishment in western Germany (Werner *et al.* 1991). After a further 30 years with low dispersal activity (Fig. 1b) the first occurrence at railway stations in South Limburg seems to be the start of its dispersal by trains, further facilitated by train frequency and long-distance travel of the same train carriage.

Dispersal by trains

What are the prerequisites for dispersal by trains? Plants growing at 1–2 m distance of the rails are heavily shaken by the air turbulence of passing trains so that ripe achenes will be taken further away from the parent plant than at release in a calm atmosphere (Table 4). This turbulence may increase the potential for further dispersal by wind because the achene will be lifted several metres above soil level; in particular, the extension on a local scale will profit from passing trains as shown for the various dispersal centres at the railway stations of Maastricht, Amsterdam, Hengelo and Zaandam, and the population dynamics at the Hoofddorp sites (Fig. 2).

To take advantage of a long-distance lift by train demands a combination of events. (1) The train has to remain long enough for loading with achenes from plants growing in the vicinity of the rails. (2) Achenes have to stay on the outside of a train during the travel at velocities above 120 km h^{-1} . (3) At the final destination of the train they have to be removed by mechanical impact because a strong fixation to the train exterior makes an autogenous release of the achenes unlikely. The presence of *S. inaequidens* at shunting-yards and train cleaning-stations of train terminals and the scarce occurrence at passing stations, especially small ones, emphasize the importance of the exposure time of the trains to dispersing achenes. The adhesion to and the travel with the train are chance processes. The presence of a pappus will render the fixation to 'safe sites' of a train, e.g. buffers and couples of railway carriages, more difficult for achenes, but oil remnants may facilitate the adhesion. The low achene mass and the pappus will increase the chance of rapid removal by air turbulence of the moving train and thus enhance a low distance dispersal. Specimens collected at the railway stations of Valkenburg (1975), Schaesberg (1977) and Elsloo-Beek (1978) may support an early achene release from a train near the achene-loading site. The scarcity of new founder

populations at railway stations and the absence along railways are further good evidence for the low chance of a long-distance lift on a train. Nevertheless, passenger trains with continuous railway carriages from Valkenburg (Limburg) to Amsterdam and Haarlem (herbarium specimen from 1981) may have helped to realize such 'undisturbed' long-distance travel (220 km). In the case of the Amsterdam population it can not be excluded that the achenes were transported by international trains from western Germany, because populations of *S. inaequidens* were recorded in 1981 at Cologne Central Station (Werner *et al.* 1991), resulting in a travel distance of 250 km. However, the gene pool of the Cologne population may be the same as that of the Limburg population because the parent plants of this population are expected to have their origin also at Liège (Werner *et al.* 1991).

The passage of trains over bridges and through tunnels will expose the achenes to increased air turbulence, enhance their release from the train and diminish the chance of arriving at a train's terminal. This may explain the late occurrence of *S. inaequidens* along the line Amsterdam–Lelystad (bridge across the IJmeer) and along the line Amsterdam–Hoorn (former bridge across, now a long tunnel below the North Sea Channel) and Amsterdam–Den Helder (long tunnels). The establishment at Hoofddorp after passing the long Schiphol tunnel is remarkable and emphasizes the chance process. Washing of the railway carriages at the train cleaning-stations will result in a complete release. Therefore it is not surprising that the new founder populations with numerous individuals occur at the shunting-yard and railway cleaning station of Amsterdam and Hengelo, the latter being perhaps the result of long-distance transport from Amsterdam (1981) to Hengelo (1986). The rapid colonization of the railway tracks at Hoofddorp is a strong and the best documented evidence for trains as achene carriers. As soon as Hoofddorp Station was connected with Amsterdam Central Station, all trains passing or waiting at the shunting-yard of Amsterdam and/or Hengelo could be supplied with numerous achenes from June to December. The first release of achenes, resulting in the establishment at Hoofddorp, occurred at the terminal for trains from Amsterdam and Hengelo. The establishment of a population near the railway station Duivendrecht 3 years after the connection with Hoofddorp and Weesp may be the result of short-distance transport by trains or even by wind.

The origin of *S. inaequidens* at other train terminals in The Netherlands may be the Amsterdam population, especially the direct trains to Leeuwarden (herbarium specimen from 1985) and to Hoorn (from 1993 on railway embankments). Despite the frequent daily trains from Amsterdam to the Head of North Holland (Den Helder; Enkhuizen) *S. inaequidens* has not arrived at these terminals. The well-developed railway vegetation at the terminals and the shunting-yards of Den Helder and Enkhuizen exclude elimination by herbicides which may be the reason for its failure at other stations, e.g. the shunting-yard at Uitgeest. The very recent population at Winschoten (Van der Meijden *et al.* 1994) may have its origin either in achenes from the Amsterdam population or in the strongly expanding founder population at Bremen (Kuhbier 1996) via international train transport. Absence at potential sites may also be due to the spraying of herbicides (railways near Uitgeest, Wormer and Castricum).

The colonization of only open sites at railways, the borderline of cycle tracks and roadsides, open patches in lawns, grassland and river banks, and derelict land in industrial areas near railways support the idea that *S. inaequidens* is a typical r-strategist being sensitive to competition for light and water. The obviously low demand for the major nutrients, nitrogen and phosphorus, enhances the colonization of nutrient poor,

but in the summer warm (micro)environments. Achene consumption by granivorous birds, as observed at the experimental dispersal site, and by seed-predating heteropterans, e.g. *Nysius senecionis* and *Stictopleurus punctatonevrosus* (Werner 1993)—not (yet) observed at railway populations in The Netherlands despite the co-occurrence of their indigenous hosts *S. jacobaea* and *S. viscosus*—and folivorous caterpillars of *T. jacobaeae* may be biological means which may contribute in the long term to the regulation of the population size.

In conclusion, a combination of favourable environmental changes together with selection to adverse climatic situations may be responsible for the rapid dispersal of this South African neophyte in Europe after a long lag-phase. Its dispersal biology has kept the anemochory, but extended to zoochory (the fixation to fleece in South Africa) and anthropochory in Europe. The success of such invaders, starting with very few individuals, may help to re-evaluate hypotheses concerning the impact of small population sizes and habitat fragmentation on survival of endangered species (Young *et al.* 1996).

ACKNOWLEDGEMENT

I thank Dr R. van der Meijden for the access to the collection of *S. inaequidens* at the Rijksherbarium in Leiden (Boxes 936 and 937).

REFERENCES

- Adema, F. & Mennema, J. (1978): *Senecio inaequidens* DC., een nieuwe Zuidlimburgse plants. *Gorteria* **9**: 111–116.
- Andersen, M.C. (1992): An analysis of variability in seed settling velocities of several wind-dispersed Asteraceae. *Am. J. Bot.* **79**: 1087–1091.
- Bicchi, C., Caniato, R., Tabacchi, R. & Tsoupas, G. (1989): Capillary gas chromatography/positive and negative ion chemical ionization mass spectrometry on pyrrolizidine alkaloids of *Senecio inaequidens* using ammonia and hydroxyl ions as the reagent species. *J. Nat. Prod.* **52**: 32–41.
- Bostock, S.J. (1978): Seed germination strategies of five perennial weeds. *Oecologia* **36**: 113–126.
- Brandes, D. (1993): Eisenbahnanlagen als Untersuchungsgegenstand der Geobotanik. *Tuexenia* **13**: 415–444.
- Brennenstuhl, G. (1995): *Senecio inaequidens* DC. bei Salzwedel -Neu für Sachsen-Anhalt. *Flor. Rundbr.* **29**: 181–183.
- Büscher, D. & Loos, G.H. (1993): Neue Beobachtungen zur Ausbreitung von *Senecio inaequidens* DC. in Westfalen. *Flor. Rundbr.* **27**: 41–49.
- Cavers, P.B. & Steel, M.G. (1984): Patterns of change in seed weight over time on individual plants. *Am. Nat.* **124**: 324–335.
- Comes, H.P. & Kalderet, J.W. (1996): Genetic basis of speed of development in *Senecio vulgaris* L. var. *vulgaris*, *S. vulgaris* ssp. *denticulatus* (O.F. Muell.) P.D. Sell, and *Senecio vernalis* Waldst. & Kit. *Heredity* **77**: 544–554.
- De Jong, T.J. & Klinkhamer, P.G.L. (1985): *Population Ecology of the Biennials Cirsium vulgare and Cynoglossum officinale: an experimental approach*. Doctorate Thesis, University of Leiden, Leiden.
- Drake, J.A., Mooney, H.A., Di Castri, F., Groves, R.H., Kruger, F.J., Rejmanek, M. & Williamson, M. (1989): *Biological Invasions: a global perspective*. Wiley & Sons, Chichester.
- Duistermaat, L. (1994): Verspreiding van *Senecio inaequidens* (Bezemkruiskruid) 1989–1991. *FLO-RON-katern* **7**: 52.
- Ernst, W.H.O. (1981): Ecological implications of fruit variability in *Phleum arenarium* L. an annual dune grass. *Flora* **171**: 387–398.
- Ernst, W.H.O. & Kessler, A. (1995): Verspreidingsoecologie. In: Bakker, K., Mook, J.H. & Van Rhijn, J.G. (eds.): *Oecologie*, 112–132, Bohn, Stafleu, Van Loghum, Houten.
- Griese, D. (1996): On the spreading of *Senecio inaequidens* DC along motorways in northeastern Germany. *Braunschweiger Naturk. Schr.* **5**: 193–204.
- Harper, J.L., Lovell, P.H. & Moore, K.G. (1970):

- The shapes and sizes of seeds. *Annu. Rev. Ecol. Syst.* 1: 327–356.
- Hedrick, P.W. (1984): *Population Biology. The evolution and ecology of populations*. Jones & Bartlett, Boston.
- Hilliard, O.M. (1977): *Compositae in Natal*. University of Natal Press, Pietermaritzburg.
- Hurka, H., Krauss, R., Reiner, T. & Wöhrmann, K. (1976): Das Blühverhalten von *Capsella bursa-pastoris* (Brassicaceae). *Plant Syst. Evol.* 125: 87–95.
- Jäger, E.J. (1988): Möglichkeiten der Prognose synanthroper Pflanzenausbreitungen. *Flora* 180: 101–131.
- Joenje, W. (1987): Remarks on biological invasions. *Proc. Kon. Ned. Akad. Wetensch. Ser. C. Biol. Med. Sci.* 90: 15–29.
- Kehren, W. (1995): Ausbreitungstendenzen von *Senecio inaequidens* DC im Stadtbereich von Köln-Deutz (MTB 5007 Köln). *Flor. Rundbr.* 29: 177–180.
- Koster, A. (1986): Bijzondere planten langs het Amsterdamse spoor. *Natura* 83: 91–99.
- Koster, A. (1991): *Spoorwegen, toevluchtsoord voor plant en dier*. Uitgeverij Kon. Ned. Natuurhist. Ver. Utrecht.
- Kuhbier, H. (1977): *Senecio inaequidens* DC—ein Neubürger der nordwestdeutschen Flora. *Abh. Naturwiss. Ver. Bremen* 38: 383–396.
- Kuhbier, H. (1996): 100 years *Senecio inaequidens* in Bremen. *Abhandl. Naturwiss. Ver. Bremen* 43: 531–536.
- Lousley, J.E. (1961): A census list of wool aliens found in Britain, 1946–1960. *Proc. Bot. Soc. Brit. Isles* 4: 221–247.
- Mazomeit, J. (1991): *Senecio inaequidens* DC—Nun auch in Baden, im Saarland und in der Pfalz. *Flor. Rundbr.* 25: 37–39.
- Mennema, J., Quène-Boterendbrood, A.J. & Plate, C.L. (1985): *Atlas van de Nederlandse Flora. 2. Zeldzame en vrij zeldzame planten*. Bohn, Scheltem & Holkema, Utrecht.
- Moll, W. (1989): Zur gegenwärtigen Verbreitung von *Senecio inaequidens* im nördlichen Rheinland. *Flor. Rundbr.* 22: 101–103.
- Mosseray, R. (1936): Matériaux pour une flore de Belgique. V. Genre *Senecio*. *Bull. Jard. Bot. Nat. Belg.* 14: 57–82.
- Rothschild, M., Aplin, R.T., Cockrum, P.A., Edgar, J.A., Fairweather, P. & Lees, R. (1979): Pyrrolizidine alkaloids in arctiid moths (Lep.) with a discussion on host plant relationships and the role of these secondary plant substances in the Arctiidae. *Biol. J. Linn. Soc.* 12: 305–326.
- Rozijn, N.A.M.G. & Van Andel, J. (1985): Analysis of the germination syndrome of some dune annuals. *Flora* 177: 175–185.
- Silvertown, J. (1989): The paradox of seed mass and adaptation. *Trends Ecol. Evol.* 4: 24–25.
- Soldaat, L.L. (1991): Nutritional Ecology of *Tyria jacobaeae* L. Doctorate Thesis, University of Leiden, Leiden.
- Stieglitz, W. (1977): Bemerkenswerte Adventivarten aus der Umgebung von Mettmann. *Gött. Flor. Rundbr.* 11: 45–49.
- Tammaro, F. & Giglio, E. (1994): Florula e vegetazione di ambienti macerioso-ruderali nei dintorni di L'Aquila e della discarica comunale. *Allionia* 32: 275–285.
- Ter Borg, S.J. (1985): Population biology and habitat relations of some hemiparasitic Scrophulariaceae. In: White, J. (ed.): *The Population Structure of Vegetation*, pp. 463–487, Junk, Dordrecht.
- Van der Goot, V.S. (1981): *De Zweefvliegen van Noordwest-Europa en Europees Rusland, in het bijzonder van de Benelux*. Kon. Ned. Natuurhist. Ver. Utrecht.
- Van der Meijden, E. (1979): Relaties tussen de Sint Jacobsvlinder en het Jacobskruiskruid. Doctorate Thesis, University of Leiden, Leiden.
- Van der Meijden, R. (1996): *Heukel's Flora van Nederland*. Wolters-Noordhoff, Groningen.
- Van der Meijden, R., Holwerda, W.J., Vermeulen, J.J. & Weeda, E.J. (1994): Nieuwe vondsten van zeldzame planten in 1991 en 1992. *Gorteria* 19: 117–162.
- Van Ooststroom, S.J. & Reichgelt, T.J. (1958): Adventieven langs de Maas in Limburg. *Natuurhist. Maandblad* 47: 67–70.
- Werner, D.J. (1993): Heteropteren an ruderalen Pflanzenarten der Gattung *Senecio*. *Verh. Westdeutsch. Entomol. Tagung* 1993 Düsseldorf.
- Werner, D.J., Rockenbach, T. & Hölscher, M.L. (1991): Herkunft, Ausbreitung, Vergesellschaftung und Ökologie von *Senecio inaequidens* DC unter besonderer Berücksichtigung des Köln-Aachener Raumes. *Tuexenia* 11: 73–107.
- Witte, L., Ehmke, A. & Hartmann, T. (1990): Interspecific flow of pyrrolizidine alkaloids. *Naturwissenschaften* 77: 540–543.
- Young, A., Boyle, T. & Brown, T. (1996): The population genetic consequences of habitat fragmentation for plants. *Trends Ecol. Evol.* 11: 413–418.