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# On the phytosociological affiliations of an invasive species *Senecio inaequidens* in Berlin

**Fytocenologická příslušnost invazního druhu *Senecio inaequidens* v Berlíně**

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During the years 1996–2001 phytosociological relevés were made of stands containing *Senecio inaequidens* in the city of Berlin and its surrounding. Data on the structure of the stands were recorded, life form spectra and ecological indicator values were calculated. This species, previously not known in the region before 1993, was found in 9 different phytosociological units (allliances). Growth parameters of *S. inaequidens* differed widely between these units and were positively correlated with cover and height of the surrounding vegetation. The conclusion drawn was that this species is one of the driving forces in the development from annual to perennial vegetation and has a role similar to that of other dominant species. From the indicator values of the stands surrounding *S. inaequidens* the following Ellenberg indicator values for the species were derived: Light L 8, temperature T 6, continentality K 4, moisture F 4, soil reaction R 7, nitrogen N 0 (= vague), and hemeroby values H α- and β- euhemerobic. Comparisons with data in literature from W and NW Germany show a broader sociological and ecological amplitude of *S. inaequidens* in this area, which was colonized by this species in the 1970s. The geographical expansion of this species is not yet finished, and further colonization within its area of distribution is likely to occur in plant communities with low degrees of hemeroby and growing in moister habitats.

Keywords: Urban plant communities, invasion, *Senecio inaequidens*, ecological indicator values, Berlin, Germany

## Introduction

*Senecio inaequidens* DC. (*Asteraceae*) is a 60–100 cm high perennial herb (Wagenitz 1987, Werner et al. 1991). Usually it hibernates as a chamaephyte, but the amount of remaining green parts depends on temperature (Ernst 1998) and the species can overwinter as a hemicryptophyte. The flowering and fruiting period is extremely long. According to Ernst (1998) achenes survived frost periods of –15° C. The original habitat of the plant are grasslands in the “highveld” (ca 1400–2800 m) of Transvaal and Natal (South Africa), but in secondary habitats it occurs widely in other parts of Southern Africa (Hilliard 1977, Werner et al. 1991, Meusel & Jäger 1992).

It was introduced into Europe in 1889 as a wool alien, initially near Hannover, Germany (Brandes 1910) and then into countries like Belgium, France, Great Britain, Italy, Spain and The Netherlands (Wagenitz 1987, Guillerm et al. 1990, Ernst 1998, Brandes 1999), recently (after 1990) also in the Czech Republic (Pyšek et al. 2002), Denmark (Skovgaard 1993), Finland (Kurtto & Helynranta 1998 sec. Gruber 1999), Norway (Often 1997), Poland (Ernst 1998) and Sweden (Ljungstrand 2000).

The process of invasion in Germany was documented carefully because the species has a very showy inflorescence, which is visible even in early winter (Wagenitz 1987, Werner et al. 1991, Kuhbier 1996, Ernst 1998, Werner 1999/2000). The invasion showed several periods. After eighty years of little escalation in distribution the species started to spread rapidly shortly before 1970 in the area of Bremen (Kuhbier 1977) and briefly after 1970 in the area of Cologne and Aachen (Werner et al. 1991). Since then it has invaded large parts of Germany (Wagenitz 1987, Werner et al. 1991, Meusel & Jäger 1992) colonizing a great variety of Central European plant communities. It colonized habitats like urban and industrial ruderal sites, sand and gravel pits, roadsides, walls, and to some extent also disturbed grasslands, heathlands, wetlands and tree plantations (Hülbusch & Kuhbier 1979, Winkelmann 1989, Werner et al. 1991). Highways and railways were most important in the initial colonization of an area (Griese 1996, Radkowitsch 1997).

Phytosociological studies (Hülbusch & Kuhbier 1979, Werner et al. 1991, Hard 1993, Kuhbier 1996) documented the presence of *S. inaequidens* in vegetation classes like *Chenopodietea, Plantaginetea, Artemisietea, Sedo-Scleranthetea, Agropyretea, Molinio-Arrhenatheretea* and marginally also in *Agrostietea stoloniferae, Bidentetea, Epilobietea* and *Salicetea*.

In the area of Berlin the first specimens were observed in 1993 (König 1995). The numbers increased slowly in the following few years (Bornkamm & Prasse 1999) and then strongly up to 2001 (Bornkamm 2002). This presented a good chance to study the distribution and phytosociological affiliation of the species from the very start of the colonization. In the present paper the invasion of plant communities was studied by phytosociological relevés. The indicator values for ecological factors were used to place *S. inaequidens* in a system of indicator values and provide data for using this species as a bioindicator. Analysis of the life forms involved is used to clarify the performance of the species in plant communities of different life form composition.

## Methods

In October and November 1996 phytosociological relevés were made in all accessible stands where *S. inaequidens* occurred. In 1997–2000 further stands, with varying species combinations, were added (altogether 95). Values of Braun-Blanquet scale were transformed to cover using the following scale: r, + = 1%, 1 = 2.5%, 2 = 15%, 3 = 38%, 4 = 63%, 5 = 88%. Most stands showed a small scale mosaic pattern and many of them were only fragmentarily developed. For this reason, and because most attention was paid to specimens of *S. inaequidens* and their immediate surroundings, relevé areas were small ( 1 to 4 m$^2$). The phytosociological analysis was not carried out down to the level of associations but vegetation units were identified mostly at the level of alliances. The names of the species and syntaxa follow Oberdorfer (1990).

The indicator values for soil moisture (F), soil reaction ( R), nitrogen (N), light (L), temperature (T) and continentality (K) were used according to Ellenberg et al. (1991). The indicator values for the degree of hemeroby were taken from Frank & Klotz (1990) and were converted into numbers in the following way: oligohemerobic = 2, mesohemerobic = 3, β-euhemerobic = 4, α-euhemerobic = 5, and polyhemerobic = 6. Frank & Klotz 1990 give ranges of values rather than single values. If the range comprised 2 values one of them was used at random, in the case of 3 values the middle value was taken and in the case of four values it was regarded as zero (=vague). For all indicator values the medians were calculated for the phytosociological units. In the rare cases where the median resulted in two differing figures the higher value was chosen. During the calculations *S. inaequidens* was not taken into account (this follows the procedure of Trepl 1984 in his investigations on *Impatiens parviflora* DC.).

In the stands the following structural data were recorded: species diversity, total cover (% area) and height of the vegetation (m); cover (% area), relative cover (% of total cover), number of individuals ($m^{-2}$), mean size of one individual (= cover of *S. inaequidens* expressed in $dm^2$/number of individuals) and height (m) of *S. inaequidens.* The proportion of species with particular life forms was calculated for the vegetation units and based on species covers. The following life forms were distinguished: therophytes, biennials, dicotyledonous hemicryptophytes and geophytes, monocotyledonous hemicryptophytes and geophytes, chamaephytes and phanerophytes. Hemicryptophytes and geophytes were combined because true geophytes were very rare and in several cases the two life forms (e.g. rhizomatous grasses) are very similar and difficult to distinguish. *S. inaequidens* was not included in this analysis.

The relationship between the structural parameters and plant communities, between life forms and plant communities and also between the indicator values and communities were analysed by Kruskal-Wallis one-way ANOVA followed by Mann-Whitney U test. The Pearson correlation coefficients were calculated from the log-transformed structural data. In all cases the level of significance was $p = 0.01$.

## Results

In Berlin *S. inaequidens* first colonized railway areas and highways, and then roadsides, cemeteries and gardens (Bornkamm & Prasse 1999, Bornkamm 2002). Nevertheless it invaded a large number of plant communities (Table 1) such as typical ruderal pioneer vegetation (*Sisymbrion, Salsolion*), trampled sites (*Polygonion*), disturbed meadows (*Arrhenatheretalia)*, ruderal grassland mainly on roadsides (*Convolvulo-Agropyrion)*, and tall herbaceous vegetation (*Dauco-Melilotion*, *Arction).* The species even grows among young shrubs (initial *Ailanthus* shrub and *Sambuco-Salicion)*, but never in dense thickets or in deep shade of trees.

The correlation analysis shows that the structural parameters were not independent from each other (Table 2). In the stands generally total cover and height are positively related. Both total cover and relative cover of *S. inaequidens* decreased with increase in number of other species, whereas its height increased with stand cover and height of surrounding vegetation. Height of *S. inaequidens* increased with its cover and size, as did the number of individuals per sqm with cover of the species.

The parameters significantly differed between vegetation units (Table 3). *Salsolion, Sambuco-Salicion* and *Convolvulo-Agropyrion* form a group with few species (9–10), whereas *Polygonion, Arrhenatheretalia* and *Dauco-Melilotion* had values of between 15 and 17 species per relevé. Since the variation was large, there were only few significant differences between members of these two groups (Table 4).

Table 1. – Plant communities in and around Berlin containing *Senecio inaequidens.* The figures represent mean cover values (0 means < 0.5) and class of constancy (I – V). Vegetation units: Pol *Polygonion avicularis,* Sis *Sisymbrion*, Sal *Salsolion ruthenicae*, Arr *Arrhenatheretalia elatioris*, Dau *Dauco-Melilotion*, Con *Convolvulo-Agropyrion*, Arc *Arction*, Ail *Ailanthus* shrub, Sam *Sambuco-Salicion.* Localities: A Highways (Autobahnen), B Cemetery St. Hedwig's Cathedral (Berlin-Mitte), C Station Berlin East (Ostbahnhof), D Goods Station Wuhlheide (Berlin-Pankow), E Goods Station Brandenburg, F Rauchstraße industrial area (Berlin-Spandau), G Station Berlin North (Nordbahnhof), H Station Berlin-Steglitz.

| Phytosociological unit | Pol | | Sis | | Sal | | Arr | | Dau | | Con | | Arc | | Ail | | Sam | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Number of relevés | 9 | | 9 | | 14 | | 11 | | 12 | | 13 | | 14 | | 6 | | 7 | |
| Localities | B | | BCDEG | | BCEFG | | A | | AB | | AEFGH | | ABCEF | | BGH | | CH | |
| *Senecio inaequidens* | 2 | V | 14 | V | 14 | V | 3 | V | 5 | V | 19 | V | 11 | V | 15 | V | 8 | V |
| Indicator species | | | | | | | | | | | | | | | | | | |
| *Polygonum aviculare* agg. | 7 | V | 0 | II | 0 | I | 1 | III | 0 | I | | | 2 | II | 0 | I | | |
| *Poa annua* | 4 | V | 3 | III | | | 0 | I | 0 | I | | | 0 | I | | | | |
| *Plantago intermedia* | 5 | III | | | | | | | | | | | | | | | | |
| *Herniaria glabra* | 2 | IV | 0 | I | | | | | 0 | I | | | 0 | I | | | | |
| *Rumex acetosella* | 4 | II | | | | | 0 | II | 1 | III | 0 | I | 0 | I | | | | |
| *Setaria viridis* | 3 | V | 3 | IV | 3 | II | 0 | I | 1 | III | 0 | I | 1 | III | 0 | I | | |
| *Sagina procumbens* | 1 | III | | | | | | | | | | | | | | | | |
| *Bromus tectorum* | | | 4 | III | 2 | IV | | | 1 | I | 1 | II | 3 | II | 1 | II | 0 | I |
| *Sisymbrium loeselii* | 0 | II | 4 | III | | | 2 | I | 0 | III | | | 1 | II | 2 | II | | |
| *Arenaria serpyllifolia* | 2 | V | 4 | III | 1 | III | | | 1 | IV | 1 | II | 0 | II | 1 | II | | |
| *Solanum nigrum* | 1 | III | 3 | I | | | 0 | I | | | 0 | I | 2 | II | 2 | I | | |
| *Cerastium holosteoides* | | | 3 | I | | | 0 | I | | | | | | | | | 0 | I |
| *Lactuca serriola* | 1 | III | 2 | III | 0 | I | | | 0 | III | 0 | I | 0 | I | 0 | II | | |
| *Plantago indica* | 0 | II | 2 | III | 1 | II | 0 | I | 1 | III | 0 | II | 0 | I | | | | |
| *Kochia scoparia* | | | 1 | I | 7 | IV | | | | | | | | | | | | |
| *Conyza canadensis* | 2 | V | 3 | IV | 6 | V | 4 | V | 2 | V | 2 | III | 1 | IV | 2 | V | 0 | II |
| *Senecio viscosus* | 2 | III | 1 | III | 3 | IV | 1 | II | 0 | I | 0 | II | 0 | I | | | | |
| *Salsola kali* subsp.*ruthenica* | 0 | II | 0 | I | 2 | IV | 1 | III | 0 | I | | | | | 0 | I | | |
| *Eragrostis minor* | 0 | I | 0 | II | 1 | II | 0 | I | | | 0 | I | | | | | | |
| *Erigeron acer* | 0 | I | | | 1 | I | | | | | | | | | | | | |
| *Festuca rubra* | | | | | | | 14 | V | 3 | II | 0 | I | 1 | I | 1 | II | | |
| *Lolium perenne* | 1 | II | 0 | I | 2 | I | 9 | III | | | 0 | I | 0 | I | | | | |
| *Agrostis tenuis* | 0 | I | | | | | 5 | II | 1 | II | | | | | | | | |
| *Poa pratensis* subsp.*irrigata* | | | 2 | II | | | 2 | II | 1 | III | 1 | I | 0 | I | 1 | I | | |
| *Trifolium repens* | | | 0 | I | | | 1 | II | 0 | II | | | 0 | I | | | | |
| *Dactylis glomerata* | | | | | | | 1 | I | | | | | | | | | | |
| *Oenothera biennis* agg. | 2 | IV | 0 | II | 1 | I | 1 | III | 36 | V | 1 | II | 6 | III | 12 | III | 0 | I |
| *Echium vulgare* | | | | | | | 0 | I | 6 | II | | | | | | | | |
| *Berteroa incana* | | | 3 | I | | | 0 | I | 3 | I | 1 | I | 0 | I | | | | |
| *Melandrium album* | 0 | I | 0 | I | 0 | I | 0 | I | 1 | IV | | | 0 | II | 0 | I | | |
| *Elymus repens* | | | | | | | 0 | I | 6 | III | 6 | II | 1 | I | 1 | I | | |
| *Poa compressa* | | | 0 | I | 0 | I | | | 0 | I | 9 | IV | 2 | II | 2 | II | 3 | III |
| *Astragalus cicer* | | | | | | | | | | | 7 | I | | | | | | |
| *Equisetum arvense* | | | | | | | 0 | I | | | 5 | I | 0 | I | | | | |
| *Potentilla argentea* | | | | | | | | | 0 | I | 5 | I | | | 0 | I | | |
| *Crepis capillaris* | | | | | 0 | I | 0 | I | | | 2 | II | 0 | I | | | | |
| *Urtica dioica* | 0 | I | 0 | II | 0 | I | | | 1 | II | | | 12 | III | 1 | I | | |
| *Artemisia vulgaris* | 1 | III | 1 | III | 0 | I | 1 | III | 3 | IV | 2 | IV | 9 | IV | 11 | V | 2 | III |
| *Solidago canadensis* | 1 | III | 1 | II | 0 | I | 0 | I | 0 | II | 1 | I | 8 | IV | 6 | II | 6 | III |
| *Tanacetum vulgare* | | | | | | | 1 | II | 1 | I | 0 | I | 3 | II | | | | |
| *Rumex thyrsiflorus* | 0 | I | 0 | II | 2 | III | | | 0 | I | 0 | I | 2 | II | 1 | II | 0 | I |
| *Daucus carota* | | | 1 | II | 0 | II | 0 | I | | | 0 | I | 2 | III | | | 0 | II |

| | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Artemisia scoparia* | | | | | | | | | | | | | 1 | I | | | | |
| *Centaurea ×psammogena* | | | | | 0 | I | | | | | | | 1 | I | | | 0 | I |
| *Ulmus pumila* | | | | | | | | | | | | | | | 14 | II | | |
| *Ailanthus altissima* | | | | | | | | | | | | | | | 13 | IV | | |
| *Saponaria officinalis* | 0 | II | | | | | | | | | | | 0 | I | 5 | I | 1 | I |
| *Humulus lupulus* | | | 0 | I | | | | | | | 0 | I | 0 | I | 3 | I | | |
| *Linaria vulgaris* | | | | | 0 | I | | | 0 | II | 0 | I | 0 | I | 3 | I | | |
| *Parthenocissus quinquefolia* | | | | | | | | | | | | | | | 2 | I | | |
| *Poa nemoralis* | | | | | | | | | 1 | II | | | 0 | I | 2 | I | | |
| *Sambucus nigra* | | | | | 0 | I | | | 0 | I | 0 | I | | | | | 27 | III |
| *Clematis vitalba* | | | | | 0 | I | | | | | 1 | II | 0 | I | | | 20 | III |
| *Calamagrostis epigejos* | | | 0 | II | 0 | I | 0 | I | 0 | I | 3 | II | 2 | II | 5 | IV | 14 | IV |
| *Robinia pseudoacacia* | | | | | | | | | | | | | | | | | 9 | III |
| *Geranium robertianum* | | | | | | | | | | | | | | | | | 6 | III |
| *Salix caprea* | | | | | | | | | 0 | I | | | | | | | 3 | III |
| *Acer platanoides* | | | | | | | | | 0 | I | 0 | I | 0 | I | 0 | II | 3 | II |
| *Acer negundo* | | | | | 0 | I | | | | | 0 | I | | | 0 | I | 2 | II |
| *Cornus sanguinea* | | | | | | | | | | | | | | | | | 2 | III |
| *Carex spicata* | | | | | | | | | | | | | | | | | 1 | I |
| Other species | | | | | | | | | | | | | | | | | | |
| *Lamium purpureum* | 0 | II | | | 0 | I | | | 0 | I | | | | | | | | |
| *Parietaria pennsylvanica* | 0 | II | | | 1 | I | | | | | | | 0 | II | | | | |
| *Stellaria media* | 0 | I | 0 | I | | | 0 | II | 0 | I | 4 | I | 0 | II | | | | |
| *Plantago major* | 0 | II | 0 | I | 0 | II | 1 | IV | | | | | 0 | I | | | | |
| *Sedum acre* | 1 | IV | 1 | II | | | | | 2 | III | 2 | I | 0 | II | 1 | I | | |
| *Chenopodium album* agg. | 2 | V | 1 | IV | 0 | I | 2 | IV | 1 | III | | | 0 | II | 3 | III | | |
| *Hypericum perforatum* | 0 | I | 0 | I | 0 | I | 0 | I | 1 | III | 0 | II | 1 | II | 0 | I | 0 | II |
| *Convolvulus arvensis* | 0 | II | | | | | | | 0 | II | 0 | I | 2 | I | 1 | III | 0 | I |
| *Atriplex patula* | 0 | I | | | | | 0 | II | | | 0 | I | 0 | I | | | 0 | I |
| *Taraxacum officinale* | 0 | III | 0 | I | 1 | II | 0 | II | 0 | II | 2 | IV | 1 | IV | 2 | II | 0 | III |
| *Polygonum convolvulus* | | | 3 | II | | | 0 | I | 0 | II | | | | | | | | |
| *Cirsium arvense* | | | 0 | I | 0 | I | | | 0 | I | 0 | I | | | | | | |
| *Tragopogon dubius* | | | 0 | I | 0 | I | | | | | 0 | I | | | | | | |
| *Matricaria perforata* | | | 1 | II | 0 | I | 1 | IV | 0 | II | 1 | I | | | | | | |
| *Hieracium laevigatum* | | | 0 | II | 0 | I | | | | | 0 | I | | | | | | |
| *Amaranthus retroflexus* | | | 0 | II | 0 | II | 0 | I | 0 | I | | | 0 | I | | | | |
| *Medicago lupulina* | | | 0 | III | 1 | I | 0 | II | | | 0 | I | 0 | I | 0 | I | | |
| *Sonchus oleraceus* | | | 3 | II | | | 2 | IV | | | 0 | I | 0 | I | 0 | I | | |
| *Acer pseudoplatanus* | | | 0 | I | | | 1 | I | 1 | III | 0 | I | 1 | I | 1 | III | | |
| *Achillea millefolium* | | | 0 | II | | | | | 2 | II | 0 | II | 0 | I | 0 | I | 0 | II |
| *Fraxinus excelsior* | | | 0 | I | | | | | 0 | I | | | | | 0 | I | 0 | I |
| *Chaenorrhinum minus* | | | | | 0 | I | 0 | I | | | 0 | I | | | | | | |
| *Reseda luteola* | | | | | 0 | I | | | | | 0 | I | 0 | I | | | | |
| *Picris hieracioides* | | | | | 0 | I | 0 | I | | | | | 0 | I | | | | |
| *Medicago sativa* | | | | | | | 0 | I | 0 | I | | | | | | | 0 | I |
| *Verbascum phlomoides* | | | | | | | | | 0 | I | 0 | I | 0 | I | | | | |
| *Poa trivialis* | | | | | | | | | 0 | I | | | 0 | I | 1 | I | | |

For total cover the group consisting of *Polygonion, Sisymbrion* and *Salsolion* had mean values < 45%, which in eight cases were significantly different from that of other vegetation units. The *Sambucus* shrub had 91% total cover and differed significantly from most other units. All other vegetation units form a group with intermediate values, which were rarely significantly different. Regarding height the lowest vegetation unit (*Polygonion)*

Table 2. – Correlation between particular structural parameters calculated from vegetation relevés (see methods for detailed description). The value of correlation coefficients is shown (n is given in brackets) and the significant correlations (p < 0.01) are in bold; n.a. = calculation not applicable because the data are not independent.

| | Stand species number | Stand cover | Stand height | *Senecio* cover | *Senecio* relative cover | *Senecio* no. of plants | *Senecio* size |
|---|---|---|---|---|---|---|---|
| Stand species number | – | | | | | | |
| Stand cover | –0.13 (95) | – | | | | | |
| Stand height | –0.22 (50) | **0.55** (50) | – | | | | |
| *Senecio* cover | **–0.38** (95) | 0.18 (95) | 0.23 (50) | – | | | |
| *Senecio* relative cover | **–0.36** (95) | –0.22 (95) | 0.03 (50) | n.a. | – | | |
| *Senecio* no. of plants | –0.34 (52) | –0.25 (52) | –0.10 (32) | **0.87** (52) | **0.85** (52) | – | |
| *Senecio* size | –0.06 (32) | 0.24 (32) | 0.15 (32) | n.a. | **0.40** (32) | 0.12 (32) | – |
| *Senecio* height | –0.30 (73) | **0.45** (73) | **0.46** (35) | **0.49** (73) | **0.32** (73) | 0.23 (52) | **0.62** (30) |

Table 3. – Summary of Kruskall-Wallis ANOVAs showing the differences in structural data between vegetation units.

| Parameter | U | d.f. | p |
|---|---|---|---|
| Stand species number | 30.95 | 8 | < 0.001 |
| Stand cover | 32.63 | 8 | < 0.001 |
| Stand height | 29.86 | 8 | < 0.001 |
| *Senecio* cover | 32.27 | 8 | < 0.001 |
| *Senecio* relative cover | 30.56 | 8 | < 0.001 |
| *Senecio* no. of plants | 26.09 | 8 | 0.001 |
| *Senecio* size | 23.70 | 8 | 0.003 |
| *Senecio* height | 17.25 | 8 | 0.028 |

Table 5. – Summary of Kruskall-Wallis ANOVAs showing the differences between vegetation units in terms of participation of life forms on vegetation cover.

| Life form | U | d.f. | p |
|---|---|---|---|
| Therophytes | 65.10 | 8 | < 0.001 |
| Biennials | 41.32 | 8 | < 0.001 |
| Dicotyledonous hemicryptophytes and geophytes | 34.00 | 8 | < 0.001 |
| Monocotyledonous hemicryptophytes and geophytes | 48.81 | 8 | < 0.001 |
| Chamaephytes | 22.86 | 8 | 0.004 |
| Phanerophytes | 57.57 | 8 | < 0.001 |

Table 7. – Summary of Kruskall-Wallis ANOVAs showing the differences between vegetation units in terms of Ellenberg indicator values.

| | U | d.f. | p |
|---|---|---|---|
| Moisture | 29.23 | 8 | < 0.001 |
| Soil reaction | 26.92 | 8 | 0.001 |
| Nitrogen | 17.87 | 8 | 0.022 |
| Hemeroby | 58.18 | 8 | < 0.001 |
| Light | 37.12 | 8 | < 0.001 |
| Temperature | 29.58 | 8 | < 0.001 |
| Continentality | 36.86 | 8 | < 0.001 |

Table 4. – Structural data for the vegetation and the specimens of *Senecio inaequidens*. Means ± S.D. are shown (see Tables 1 and 2 for codes of phytosociological units and numbers of records in each case). Means bearing the same letters row-wise were not significantly different (Mann-Whitney U test). *Senecio* size was expressed as its cover / number of individuals.

| | Pol | Sis | Sal | Arr | Dau | Con | Arc | Ail | Sam |
|---|---|---|---|---|---|---|---|---|---|
| Stand species number | 15.1±2.3 a | 14.7±3.5 a | 9.1±4.7 b | 15.4±6.1 a | 16.6±3.5 a | 10.4±2.8 b | 12.6±4.4 ab | 13.7±6.0 ab | 9.1±3.8 ab |
| Stand cover | 38.3±15.8 a | 42.8±13.0 a | 47.5±18.6 ab | 54.1±29.1 abc | 58.2±21.5 abc | 49.1±21.9 abc | 68.6±25.0 bc | 78.3±18.3 c | 91.4±9.4 abc |
| Stand height (m) | 0.4±0.1 ab | 0.6±0.1 ac | 1.1±0.3 bde | 1.2±0.6 bcde | 1.2±0.7 bde | 0.7±0.4 bce | 1.0±0.3 df | 2.0±0.9 eg | 2.0±1.1 abfg |
| *Senecio* cover (%) | 1.5±0.5 ab | 14.1±9.9 acd | 20.9±17.6 ce | 3.0±2.4 b | 5.3±8.3 bcf | 19.3±17.9 de | 11.1±9.9 def | 15.3±24.4 bd | 7.7±10.2 bd |
| *Senecio* relative cover (%) | 5.0±3.0 a | 31.0±17.5 b | 44.1±30.2 c | 14.0±9.5 ad | 8.3±8.9 ac | 30.8±24.7 bcd | 18.7±16.7 abc | 16.2±23.9 abc | 7.9±10.1 abc |
| *Senecio* no. of plants/m$^{-2}$ | 1.2±0.4 a | 1.8±0.8 bc | 1.4±1.3 b | 0.6±0.6 acd | 0.8±0.4 acd | 1.1±1.4 acd | 1.6±0.8 cd | 0.7±0.3 acd | 0.5±0.3 acd |
| *Senecio* size (dm$^2$) | 21.8±0.4 a | 11.0±5.5 b | 43.5±1.0 c | 4.5±0.8 bc | 6.1±4.5 abc | 10.2±9.5 b | 5.9±5.0 abc | 8.0±8.3 abc | 13.0±13.1 abc |
| *Senecio* height (m) | 0.2±0.1 a | 0.6±0.1 a | 0.6±0.2 a | 0.5±0.2 a | 0.5±0.1 a | 0.6±0.2 a | 0.6±0.2 a | 0.8±0.3 a | 0.7±0.3 a |

Table 6. – The life form in plant communities containing *Senecio inaequidens*. Calculations are based on species covers. Means ± S.D. are shown (see Table 1 for codes of phytosociological units and the numbers of relevés recorded). Means bearing the same letter row-wise were not significantly different in Mann-Whitney U test.

| | Pol | Sis | Sal | Arr | Dau | Con | Arc | Ail | Sam |
|---|---|---|---|---|---|---|---|---|---|
| Therophytes | 64.7±14.7 a | 61.9±19.5 a | 74.4±21.1 a | 34.2±14.2 b | 13.6± 6.3 c | 22.1±21.9 bcd | 18.1±19.7 bcd | 18.2±21.0 cd | 1.8±3.1 d |
| Biennials | 6.8±4.3 ab | 9.8±7.4 abc | 5.4±7.1 abc | 6.4±11.1 ac | 47.2±15.6 | 4.6±5.6 bcd | 9.9±11.0 bcd | 11.6±17.4 bcd | 1.1±1.6 cd |
| Dicotyledonous hemicryptophytes and geophytes | 19.3±17.5 a | 11.8±12.9 a | 15.4±17.8 ac | 6.2±4.7 ad | 17.4±11.9 e | 35.2±25.9 bc | 52.1±24.6 bc | 24.3±17.5 bcde | 29.7±23.5 bcde |
| Monocotyledonous hemicryptophytes and geophytes | 2.1± 2.7 a | 8.6±10.5 abc | 4.3±11.9 ad | 48.7±18.2 ef | 14.8±13.4 bg | 29.6±20.0 beh | 7.6±10.3 acd | 16.6±17.4 acdfgh | 33.0±25.3 cfgh |
| Chamaephytes | 6.4±4.1 a | 7.0±10.9 ab | 0.5± 1.3 bc | 4.5±4.8 abd | 7.0± 5.8 abd | 7.9±9.4 abd | 11.5±15.6 abd | 16.0±11.8 abd | 4.5±7.1 abcd |
| Phanerophytes | 0.7±1.5 ab | 0.9±2.2 ac | – | – | – | 0.6± 1.9 b | 0.8± 2.6 c | 13.3±19.9 d | 29.9±23.2 d |

was only 0.35 m on average. However, as the height of various vegetation units varied greatly, even the average of 2 m for communities of shrubs only differed significantly from that of few other plant communities. All other vegetation units reached heights in the range 0.7 to 1.2 m (Table 4).

The performance of *S. inaequidens* differed in the various vegetation units. In *Polygonion* it had low cover, relative cover, and number and size of individuals. To a lesser extent the same was true for *Arrhenatheretalia*. In *Sambucion* it had low relative cover and number of individuals, but relatively large individual size. In vegetation units like *Salsolion, Convolvulo-Agropyrion* and *Sisymbrion* the species performed best with high cover values and sometimes also greater individual number and size (Table 4).

Significant differences between vegetation units occurred with respect to the participation of life forms (Table 5). Therophytes dominate in the *Polygonion, Sisymbrion* and *Salsolion* (Table 6). The same was true for the *Arrhenatheretalia* stands. Although the monocotyledonous hemicryptophytes and geophytes here were the largest group the high proportion of therophytes indicate that colonization by *S. inaequidens* occurred initially in open grassland. In *Dauco-Melilotion* biennials were most abundant, and therophytes rarest. In *Convolvulo-Agropyrion* dicotyledonous hemicryptophytes and geophytes (forbs) and monocotyledonous hemicryptophytes and geophytes (mainly grasses) occurred almost equally. The *Arction* stands were dominated by forbs. In both vegetation units therophytes were uncommon. Phanerophytes were found almost exclusively in the young shrub stands. But even in *Sambuco-Salicion* phanerophytes did not attain higher values than forbs, and even lower values in the *Ailanthus* stands. That is, the occurrence of *S. inaequidens* was restricted to very low, open stands of shrubs of early successional stages. Chamaephytes (mainly S*edum* species) were uncommon or almost absent in *Salsolion*.

It was assumed that *S. inaequidens* would have a negative effect on its main competitors or vice versa. To test for this the log-tranformed cover values of 15 species which were present in at least 20 relevés with *S. inaequidens* and had average cover values of at least 2% were checked for correlation with that of *S. inaequidens*. Only two of them were weakly significantly correlated, namely *Solidago canadensis* ($p = 0.011$) and *Artemisia vulgaris* ($p = 0.020$), but both relationships were positive.

Indicator values calculated for the vegetation units in which *S. inaequidens* occurred differed significantly between the units (Table 7). The median of the moisture value (F) was always 4 with the exception of 5 for the *Sambucus* shrub, the first quartile always 4 with the exception of 3 for *Salsolion.* The median for the soil reaction indicator value in Berlin was always 7, the lower first quartile in *Polygonion* and the higher third quartile in *Salsolion* resulted in several significant differences. The median of the nitrogen indicator value varied from 5 to 7, the quartiles from 4 to 8 but not significantly. The medians of the hemeroby values varied between 4 (β-euhemerobic) and 5 (α-euhemerobic). The higher value H5, indicating greater human activity and disturbance, was recorded in most open vegetation types, but also in early stages of the *Ailanthus* shrub. The lower values (H4) were recorded in the perennial grass and forb communities (*Convolvulo-Agropyrion*, *Arction*), and *Sambucus* shrub. The median of the light indicator value was 8 in all open vegetation units and 7 in the two shrub communities. In *Salsolion* even the first quartile was as high as 8. Both differences were significant in several cases. The median of the temperature indicator value was always 6. Lower values of the first quartile were recorded in *Sambucion,* and higher values of the third quartile in *Salsolion.* The value indicating

Table 8. Medians (M), first quartiles (Q1) and third quartiles (Q3) of the ecological indicator values (Ellenberg et al. 1991) of plant communities containing *Senecio inaequidens* displayed separately for data from the present study and from the literature. n = number of species. See text for details on how the hemeroby scale was transformed. Upper part: See Table 1 for codes of phytosociological units and numbers of relevé recorded in them. P = data from the present paper. Medians column-wise with the same letter are not significantly different (multiple range test). Lower part: We = data from Werner et al. (1991) from the region around Köln-Aachen; Wi = data from Winkelmann (1989) from near Bremen. POL *Polygonion avicularis,* SIS *Sisymbrion,* DMd *Dauco-Melilotion,* dry variants, DMf *Dauco-Melilotion,* fresh variants, SS *Sedo-Scleranthetea,* AR *Convolvulo-Agropyrion* and *Agropyro-Rumicion,* ARR *Arrhenatherion*, INS initial stages of *Buddleja davidii* shrubs, SAM *Sambuco-Salicion,* WET different wetland communities, SLX *Salicion albae,* INH initial stages of heathland, TP young plantations of *Pinus sylvestris* and *Alnus incana.*

| | | n | Moisture | | | Soil reaction | | | Nitrogen | | | Hemeroby | | | Light | | | Temperature | | | Continentality | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Q1 | M | Q3 | Q1 | M | Q3 | Q1 | M | Q3 | Q1 | M | Q3 | Q1 | M | Q3 | Q1 | M | Q3 | Q1 | M | Q3 |
| Pol | P | 44 | 4 | 4 a | 5 | 5 | 7 ab | 7 | 4 | 6 a | 7 | 4 | 5 a | 5 | 7 | 8 a | 8 | 6 | 6 ab | 6 | 3 | 4 abc | 5 |
| Sis | P | 59 | 4 | 4 ab | 5 | 6 | 7 cde | 8 | 4 | 6 a | 7 | 4 | 5 ab | 5 | 7 | 8 a | 8 | 6 | 6 ab | 7 | 4 | 5 de | 7 |
| Sal | P | 49 | 3 | 4 bc | 5 | 7 | 7 cef | 8 | 4 | 5 a | 7 | 4 | 5 a | 5 | 8 | 8 | 8 | 6 | 6 bc | 7 | 4 | 5 f | 7 |
| Arr | P | 69 | 4 | 4 a | 5 | 6 | 7 aceg | 8 | 4 | 5 a | 7 | 4 | 5 ac | 5 | 7 | 8 a | 8 | 6 | 6 ad | 6 | 3 | 4 ag | 5 |
| Dau | P | 67 | 4 | 4 a | 5 | 6 | 7 bdg | 7 | 4 | 5 a | 7 | 4 | 5 bcd | 5 | 7 | 8 a | 8 | 6 | 6 a | 6 | 3 | 4 a | 5 |
| Con | P | 64 | 4 | 4 ac | 5 | 6 | 7 adc | 8 | 4 | 5 a | 7 | 4 | 4 cde | 5 | 7 | 8 a | 8 | 6 | 6 ae | 6 | 3 | 4 a | 5 |
| Arc | P | 69 | 4 | 4 a | 5 | 7 | 7 eh | 8 | 4 | 5 a | 7 | 4 | 4 bcd | 5 | 7 | 8 a | 8 | 6 | 6 ac | 6 | 3 | 5 bdfg | 5 |
| Ail | P | 53 | 4 | 4 a | 5 | 6 | 7 adfh | 8 | 5 | 6 a | 7 | 4 | 5 ad | 5 | 7 | 7 a | 8 | 6 | 6 acf | 6 | 3 | 4 bdfg | 7 |
| Sam | P | 32 | 4 | 5 a | 5 | 6 | 7 adfh | 7 | 5 | 7 a | 8 | 3 | 4 e | 4 | 7 | 7 | 8 | 5 | 6 def | 6 | 3 | 4 ceg | 6 |
| POL | We | 42 | 4 | 4 | 5 | 6 | 7 | 7 | 4 | 6 | 7 | 4 | 5 | 5 | 7 | 7 | 8 | 6 | 6 | 6 | 3 | 5 | 5 |
| SIS | We | 49 | 4 | 5 | 6 | 6 | 7 | 7 | 5 | 6 | 7 | 4 | 5 | 5 | 7 | 7 | 8 | 5 | 6 | 6 | 3 | 3 | 5 |
| DMd | We | 62 | 3 | 3 | 4 | 5 | 6 | 7 | 4 | 5 | 7 | 3 | 4 | 5 | 7 | 8 | 8 | 6 | 6 | 6 | 3 | 3 | 5 |
| DMf | We | 59 | 4 | 5 | 6 | 6 | 7 | 8 | 5 | 6 | 7 | 3 | 4 | 5 | 7 | 7 | 8 | 5 | 6 | 6 | 3 | 3 | 5 |
| SS | We | 37 | 3 | 4 | 5 | 6 | 7 | 8 | 3 | 4 | 6 | 3 | 4 | 5 | 7 | 8 | 8 | 6 | 6 | 6 | 3 | 4 | 5 |
| AR | We | 38 | 4 | 4 | 5 | 6 | 7 | 8 | 4 | 6 | 7 | 3 | 4 | 5 | 7 | 7 | 8 | 5 | 6 | 6 | 3 | 3 | 5 |
| ARR | We | 57 | 4 | 5 | 5 | 6 | 7 | 7 | 4 | 6 | 7 | 3 | 4 | 4 | 7 | 7 | 8 | 5 | 6 | 6 | 3 | 3 | 5 |
| INS | We | 60 | 4 | 5 | 6 | 6 | 7 | 7 | 5 | 6 | 7 | 3 | 4 | 5 | 6 | 7 | 8 | 6 | 6 | 6 | 3 | 4 | 5 |
| SAM | We | 36 | 4 | 5 | 6 | 6 | 7 | 7 | 5 | 6 | 7 | 3 | 4 | 4 | 7 | 7 | 8 | 5 | 6 | 6 | 3 | 4 | 5 |
| WET | We | 52 | 5 | 7 | 8 | 5 | 7 | 8 | 4 | 6 | 7 | 3 | 4 | 5 | 7 | 7 | 8 | 5 | 6 | 6 | 3 | 3 | 4 |
| SLX | We | 37 | 5 | 7 | 8 | 5 | 7 | 8 | 4 | 6 | 7 | 3 | 4 | 5 | 7 | 7 | 8 | 5 | 6 | 6 | 3 | 4 | 5 |
| INH | Wi | 74 | 4 | 4 | 5 | 4 | 6 | 7 | 3 | 5 | 7 | 3 | 4 | 4 | 7 | 7 | 8 | 6 | 6 | 6 | 3 | 3 | 5 |
| TP | Wi | 39 | 5 | 5 | 6 | 3 | 5 | 7 | 3 | 5 | 7 | 3 | 3 | 4 | 6 | 7 | 8 | 5 | 5 | 6 | 3 | 3 | 4 |

continentality (K) had large distances between the quartiles, and the median varied between 4 and 5. The highest K values were found in *Sisymbrion* and *Salsolion,* the lowest in *Dauco-Melilotion* and *Convolvulo-Agropyrion* (Table 8).

For comparison indicator values calculated from records in the literature for W and NW Germany (Winkelmann 1989, Werner et al. 1991) are given (Table 8). These indicator values are similar to the Berlin values: the R values are predominantly 7, the T values predominantly 6, and the N values vary considerably. The K values, however, are only 3 or 4. Furthermore it is interesting to note that in several cases the F values are higher, H values lower and R values rarely lower. This means that *S. inaequidens* here extends into moister, less disturbed and sometimes also more acidic habitats.

## Discussion

Of the 140 places in the area of Berlin where *S. inaequidens* was found in 2001 90% were located along railway tracks or highways (Bornkamm 2002). Nevertheless the species occurs in a surprisingly large number of vegetation types. After only a few years the species occurred in as many plant communities as other species present in Berlin for much longer time, e.g. *Solidago canadensis* and *Solidago gigantea* (Wittig 1978). This finding can be explained by the fact that railways and to a lesser extent highways provide a great variety of habitats with differing regimes of disturbance, ranging from actual working areas to marginal sites, which are not disturbed for years.

Regarding the correlations between the different structural parameters it seems that *S. inaequidens* reacts to the conditions in the stands and also influences the vegetation. As the height of the species increased with height and total cover of the vegetation, and cover per inidividual with vegetation height, the species apparently responded to the greater cover and height of the surrounding vegetation. It did so with limited success as its relative cover did not increase with vegetation cover and height. Thus *S. inaequidens* responds to crowding in the same way as its competitors, but not in a superior way. Since, however, the number of species per relevé decreased with increasing cover, relative cover and height of *S. inaequidens,* it apparently exerted a negative influence on the species richness.

All growth parameters of *S. inaequidens*, like cover, relative cover, height and cover per inidividual increased together, and allometrically. It is interesting to note that there was no decrease in the cover per individual with increase in the number of individuals. This means that density stress did not occur.

The life forms present in the stands did not influence the performance of *S. inaequidens.* The highest values of cover and relative cover were recorded in *Sisymbrion* and *Salsolion,* which are dominated by therophytes, and also in *Convolvulo-Agropyrion,* which is dominated by perennial species. The lowest values were recorded in *Polygonion,* dominated by therophytes. *S. inaequidens* survives trampling and even mowing, but such stress prevents growth and expansion of the species. It can be concluded that it does not react to the life form of its neighbours but to the shape of canopy (and probably of the root system) as other plants do (Rebele 1996, 2000).

*S. inaequidens* has a broad sociological amplitude and is not a characteristic species of any one of the vegetation units presented in Table 1. It performs best in ruderal or disturbed herbaceous plant communities. In the course of succession from annual vegetation to woody vegetation on different ruderal soils (Bornkamm & Hennig 1982, Kowarik 1988, Pyšek & Pyšek 1991) *S. inaequidens* is both a pioneering and early successional species, which disappears in the later stages of successions. But in W and NW Germany, where *S. inaequidens* invaded 20 years earlier, the species' sociological amplitude is much broader and it also grows also in wetland and heathland communities. This may also happen in the future in recently colonized areas like the Berlin region. It is astonishing that *S. inaequidens*, a perennial species, is so widespread in pioneer plant communities. Obviously the species needs space to establish itself, and plants that germinate in spring can flower and produce offspring in the same year. This species is one of the driving forces in the development from annual to perennial vegetation, until it is shaded out by woody plants. It shows a similar behaviour to plants like *Solidago canadensis, Tanacetum vulgare* and *Artemisia vulgaris,* with the exception that it flowers abundantly in its first year. *S. inaequidens,* thus, has features typical of both annual and perennial plants. It is unlikely that it will ever dominate whole landscapes as does *Solidago canadensis*, which can persist for a long time.

Finally the mean indicator values of the vegetation units containing *S. inaequidens* were used in order to propose indicator values for this species. Indicator values for plant communities can not automatically be converted into values for single species, because the range of communities is narrower than the range of individual species (Böcker et al. 1978). But our data (Table 8) may be used for this purpose. The medians of the indicator values for light (L 8), temperature (T 6), soil reaction (R 7) and moisture (F 4) are most consistent. The indicator values for nitrogen (N) vary too greatly and the species cannot be used as an indicator in this case. The great variation in the indicator value of continentality (K) probably is due its weak definition. The differences between the values from W and NW Germany (K 3 and 4) and the Berlin region (K 4 and 5) just reflect the geographical position of the two areas. At present the European distribution of *S. inaequidens* fits best K 4: "Suboceanic, mainly Central Europe, with extensions to the East" (Ellenberg et al. 1991). In Berlin, hemeroby value is H 5, but in W and NW Germany this species has lower H and F values. This may indicate that the species eventually colonizes moister and less disturbed habitats. Lotz (1998) stated that *S. inaequidens* is dependent on the activity of man and should be classified as an epoecophyte. However, as this species also occurs rarely in more natural vegetation, where its persistence does not depend on man, it should also be classified as an agriophyte (Lohmeyer & Sukopp 1992, 2001). Summarizing, this study reveals that the following indicator values should be added to the system of Ellenberg et al. (1991) and Frank & Klotz (1990) for *S. inaequidens*: F 4, R 7, N 0 (= vague), H4 and 5 (β- and α-euhemerobic), L 8, T 6, K 4.

In future it is likely that other plant communities with lower degrees of hemeroby and moister habitats will be colonized by *S. inaequidens* in the current area of its distribution. In addition, the invasion in the range of this species is likely to continue. Since it was recently found in Scandinavia the whole coastal region of the Baltic Sea seems to be open for settlement by *S. inaequidens.*

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