Effect of pappus removal on seed germination in *Solidago ×niederederi* (Asteraceae) and closely related species

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**Abstract**

In *Solidago*, the pappus, a modified calyx, protects ovary and fruit from predation and is strongly involved in anemochory. In this study, we aimed to test the hypothesis that the mechanical removal of pappus decreases the final percentage and speed of seed germination. We examined *S. ×niederederi*, a natural hybrid between invasive *S. canadensis* and native *S. virgaurea*, in comparison to its parental species and *S. gigantea*. We conducted a 21-day germination test in the laboratory, using 50 fruits with intact pappus and 50 fruits with removed pappus in four replicates, for each taxon. The statistical analysis demonstrated that the final percentage of germinated seeds was remarkably lower in the group of fruits with removed pappus in *S. canadensis* (*p* ≤ 0.05) and *S. gigantea* (*p* ≤ 0.05). Moreover, the speed of seed germination was also significantly lower after pappus removal in *S. canadensis* and *S. gigantea*, based on the Timson’s index (*p* ≤ 0.05). In the case of *S. ×niederederi* and *S. virgaurea*, the hypothesis was rejected. We assumed that the small size of the cypselae could be responsible for the negative effect of pappus removal on seed germination.

**Keywords** Alien species · Hybrid · Pappus · Seed germination test · *Solidago* · Timson’s index

**Introduction**

The pappus, a modified calyx, plays a major role in the protection of the ovary and dispersal of fruits in *Asteraceae*. It protects the ovary and fruit from predation and is involved in anemochory and zoochory (Mukherjee and Nordenstam 2008 and references therein). Moreover, the structure and arrangement of pappus elements have long been used to delimit tribes, genera and other taxa in *Asteraceae* (Small 1918; Nesom 1993, 2000; Mukherjee and Nordenstam 2008; Marzinek and Oliveira 2010; Frangiote-Pallone and de Souza 2014; Talukdar 2015; Silva et al. 2018). Interestingly, Shaukat et al. (2004) evidenced that the removal of pappus decreases the final percentage of seed germination due to decreased hydration of the fruits in *Vernonia cinerascens* Sch. Bip. and *V. cinerea* (L.) Less. Similarly, Hale et al. (2010) proved that in the fruits with removed pappus seed germination was 31% lower than in the fruits with intact pappus in *Taraxacum officinale* F.H. Wigg.

The genus *Solidago* L. comprises about 133 species and is native to North America, South America, Europe and Asia (Semple and Cook 2006; Semple 2020). In *Solidago*, the pappus is strongly involved in anemochory and consists of barbellate bristles which can be arranged in 1–3 whorls (Hood and Semple 2003). However, there is a lack of studies that could explain the role of pappus in seed germination in this genus. *Solidago ×niederederi* Khek, a natural hybrid between the North American *S. canadensis* L. and the European *S. virgaurea* (Pliszko 2015; Karpavičienė and Radušienė 2016; Pliszko and Zalewska-Gałosz 2016; Radušienė et al. 2018), occurs in several countries in Europe and is treated as an alien taxon (Pliszko and Kostrakiewicz-Gieralt 2017b; Jazwa et al. 2018). It occupies anthropogenic habitats such as abandoned fields, roadsides, railway embankments, disused quarries, tree plantations, forest clearings, and tracks, usually together with its parental species (Nilsson 1976; Burton 1980; Sunding 1989; Stace et al. 2015; Gudžinskas and Petrlulaitis 2016; Pliszko and Kostrakiewicz-Gieralt 2017b; Pliszko et al. 2017, 2019). Similarly to *S. canadensis* and *S. virgaurea*, the hybrid is a perennial plant and spreads by wind-dispersed fruits (cypselae) (Pliszko and...
Kostrakiewicz-Giera (2017b, 2019). However, the production of fruits in S. ×niederederi is usually limited by its reduced pollen viability (Migdałek et al. 2014; Karpavičiūnė and Radušiūnė 2016). On the other hand, there is a probability that the hybrid produces the fruits by backcrossing with S. canadensis and S. virgaurea (Pagitz 2016). According to Pliszko and Kostrakiewicz-Giera (2017a, 2017b, 2018a), seeds of S. ×niederederi can achieve a high percentage of germination and cold stratification is not obligatory to break their dormancy. Since the hybrid has the potential to be established and poses a threat by competing with native species for insect pollinators and other resources (Pliszko and Kostrakiewicz-Giera 2017b, 2018b, 2019; Jaźwa et al. 2018), the studies on its ecology are needed.

In this study, we focused on the effect of pappus removal on seed germination in S. ×niederederi and its parental species. We also included S. gigantea Ait., a North American species closely related to S. canadensis. We aimed to test the hypothesis that the mechanical removal of pappus decreases the final percentage and speed of seed germination.

Materials and methods

Fruit sampling and measurements

Fruits (cypselae) of Solidago ×niederederi, S. canadensis, S. virgaurea, and S. gigantea, were collected from natural populations (one population per taxon) occurring on abandoned fields near Palcza (GPS coordinates: 49°48.500’N/19°45.187’E; 49°48.755’N/19°45.405’E; altitude: 496–546 m a.s.l.), southern Poland, on 27 October 2018. The populations of S. canadensis, S. virgaurea, and S. gigantea were isolated from each other by a distance of at least 100 m. Due to difficulties in finding a well-isolated population of S. ×niederederi we selected the F1 generation hybrids which occurred at a distance of at least 10 m from both parental species. For each taxon, ten panicles with mature fruits were randomly sampled and transported to the laboratory. In the laboratory, the panicles were kept at room temperature (+25 °C) for 5 days to dry. Next, the panicles were threshed manually to obtain the samples of fruits for further investigation. The samples of 50 well-developed fruits of each taxon were selected for measurements using a Nikon SMZ1500 stereomicroscope. The measurements included the length and the width of the cypselae (fruit body excluding the pappus), as well as the number and the length of the pappus bristles, and only one randomly selected pappus bristle from the inner whorl of each fruit was measured. The width was measured at the top of the cypselae, in the area where the fruit is the widest. For each taxon, the samples of 200 fruits whose pappus had been removed mechanically and the samples of 200 fruits with intact pappus as a control group were used for a seed germination test. The pappus bristles were carefully separated from the cypselae using the tweezers and Nikon

| Parameter                  | Formula for calculation | Description                                      |
|----------------------------|-------------------------|--------------------------------------------------|
| Timson’s index             | Σn                      | n – cumulative daily germination percentage for each day of the test |
| mean germination time      | Σ (ni → d)/N             | n – number of seeds germinated at day di, N – total number of seeds germinated in the test |
| coefficient of velocity   | 100(A1 + A2 + A3 + A4)/ (A1T1 + A2T2 + A3T3 + A4T4) | A1 + A2 + A3 + A4 – number of seeds germinated on the first, second and final days that seedlings appeared, T1, T2 and T3 – number of days between sowing and first, second and final days that seedlings were recorded |

Table 2 Differences in the mean values (±SD) of selected fruit morphological traits between Solidago ×niederederi, S. canadensis, S. virgaurea, and S. gigantea (n = 50)

| Taxon                     | Number of pappus bristles (±) | Length of pappus bristle (mm) (±) | Length of cypselae (mm) (±) | Width of cypselae (mm) (±) |
|--------------------------|-------------------------------|----------------------------------|-----------------------------|----------------------------|
| Solidago ×niederederi    | 39.5 (±6.0)b                  | 2.8 (±0.6)b                      | 1.8 (±0.2)c                  | 0.5 (±0.0)a                 |
| Solidago canadensis      | 24.9 (±3.6)b                  | 1.9 (±0.3)b                      | 1.1 (±0.1)b                  | 0.4 (±0.4)a                 |
| Solidago virgaurea       | 65.7 (±7.1)c                  | 4.0 (±0.6)c                      | 2.4 (±0.2)b                  | 0.7 (±0.1)c                 |
| Solidago gigantea        | 41.4 (±5.0)b                  | 2.8 (±0.4)b                      | 1.6 (±0.2)b                  | 0.5 (±0.0)a                 |
| Statistical significance level | F = 378.9; p < 0.001          | F = 158.7; p < 0.001             | F = 396.7; p < 0.001         | F = 8.2; p < 0.001          |

The diverse letters in superscript indicate the significant differences (Tukey post-hoc test) between the taxa.
SMZ1500 stereomicroscope to avoid the inclusion of fruits whose pericarp was damaged by removing the pappus. The accuracy of pappus removal and a lack of damage to the fruit body were checked using the Nikon SMZ1500 stereomicroscope. The studied taxa were identified based on morphological characters provided by Nilsson (1976), Karpačienė and Radušienė (2016), and Gudžinskas and Žalneravičius (2016).

Seed germination test

Sets of 50 fruits of Solidago ×niederederi, S. canadensis, S. virgaurea, and S. gigantea in four replicates were placed on filter paper in 90 mm polystyrene Petri dishes. Next, the fruits were wetted using 2.5 ml of distilled water and the moisture inside the Petri dishes was maintained by the addition of 1 ml of distilled water every other day of the germination test period. The samples were kept at room temperature (+25 °C) under a 12-h photoperiod (630 lx). The germination test lasted 21 days and the fruits were checked in one-day intervals. The seed included in the cypsela was determined as germinated when the pericarp of the cypsela was broken and the length of the emerging radicle, hypocotyl or cotyledons was at least 1 mm.

Germination parameters

The speed of seed germination was estimated using the Timson’s index (Timson 1965), the mean germination time (Orchard 1977), and the coefficient of velocity (Baskin and Baskin 2014). The formulas of germination parameters are explained in Table 1. The Timson’s index was calculated for a 10-day seed germination test period, whereas the mean germination time and the coefficient of velocity were calculated for a total time of seed germination test period (21 days). The fast seed germination is indicated by the high values of Timson’s index and coefficient of velocity as well as by the low value of the mean germination time (Al-Mudaris 1998; Baskin and Baskin 2014; Pliszko and Kostrakiewicz-Gieralt 2017a, 2017b, 2018a).

Statistical analysis

Due to a low number of replicates in the seed germination experiment the statistical analysis of germination parameters was based on the non-parametric tests. The Kruskal-Wallis H test was applied to check the statistical significance of

| Experimental group | Taxon                        | Final percentage of germinated seeds | Statistical significance level (Kruskal-Wallis H test) |
|--------------------|------------------------------|--------------------------------------|-------------------------------------------------------|
| Fruits with intact pappus | Solidago ×niederederi       | 67.0 (±5.0)ab                        | H = 12.6; p ≥ 0.01                                      |
|                     | Solidago canadensis         | 60.0 (±3.8)a                         |                                                        |
|                     | Solidago virgaurea          | 71.0 (±5.0)ab                        |                                                        |
|                     | Solidago gigantea           | 91.0 (±3.5)b                         |                                                        |
| Fruits with removed pappus | Solidago ×niederederi       | 64.5 (±9.3)ab                        | H = 11.3; p ≤ 0.05                                      |
|                     | Solidago canadensis         | 47.5 (±1.9)a                         |                                                        |
|                     | Solidago virgaurea          | 82.0 (±9.1)b                         |                                                        |
|                     | Solidago gigantea           | 68.5 (±7.2)ab                        |                                                        |

Table 3 Differences in the mean values (±SD) of final percentage of germinated seeds between Solidago ×niederederi, S. canadensis, S. virgaurea, and S. gigantea, in the groups of fruits with intact and removed pappus, on the basis of four replicates of 50 fruits

The diverse letters in superscript indicate the significant differences between the taxa

| Experimental group | Taxon                        | Timson’s index | Statistical significance level (Kruskal-Wallis H test) |
|--------------------|------------------------------|----------------|-------------------------------------------------------|
| Fruits with intact pappus | Solidago ×niederederi       | 472.5 (±44.9)ab | H = 10.7;                                             |
|                     | Solidago canadensis         | 411.0 (±17.6)a | p ≤ 0.05                                              |
|                     | Solidago virgaurea          | 418.5 (±8.5)a  |                                                        |
|                     | Solidago gigantea           | 650.5 (±40.4)b |                                                        |
| Fruits with removed pappus | Solidago ×niederederi       | 473.0 (±50.2)ab | H = 10.5;                                             |
|                     | Solidago canadensis         | 325.5 (±37.5)a | p ≤ 0.05                                              |
|                     | Solidago virgaurea          | 544.0 (±50.4)b |                                                        |
|                     | Solidago gigantea           | 493.0 (±53.7)ab|                                                        |

Table 4 Differences in the mean values (±SD) of Timson’s index between Solidago ×niederederi, S. canadensis, S. virgaurea, and S. gigantea, in the groups of fruits with intact and removed pappus, on the basis of four replicates of 50 fruits

The diverse letters in superscript indicate the significant differences between the taxa
differences between the studied taxa in (i) final percentage of germinated seeds, (ii) Timson’s index, (iii) mean germination time and (iv) coefficient of velocity in the group of fruits with intact and removed pappus. The Mann-Whitney U test was used to check the statistical significance of differences between the two experimental groups of fruits of the studied taxa in (i) final percentage of germinated seeds, (ii) Timson’s index, (iii) mean germination time and (iv) coefficient of velocity.

The normal distribution of the untransformed data of fruit morphological traits was tested using the Kolmogorov–Smirnov test, while the homogeneity of variance was checked using the Levene test at the significance level of \( p < 0.05 \). As the data were consistent with the normal distribution and the variance was homogeneous their analysis was based on the one-way analysis of variance (ANOVA) and the Tukey post-hoc test. The aforementioned analysis was applied to test the statistical significance of differences in the number and length of pappus bristles and in the length and the width of fruits between the studied taxa.

## Results

### Fruit morphological traits

Considering the number of pappus bristles and the length of pappus bristle, *Solidago ×niederederi* was similar to

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**Table 5** Differences in the mean values (±SD) of mean germination time between *Solidago ×niederederi*, *S. canadensis*, *S. virgaurea*, and *S. gigantea*, in the groups of fruits with intact and removed pappus, on the basis of four replicates of 50 fruits

| Experimental group | Taxon                  | Mean germination time | Statistical significance level (Kruskal-Wallis H test) |
|--------------------|------------------------|-----------------------|-------------------------------------------------------|
| Fruits with intact pappus | *Solidago ×niederederi* | 4.0 (±0.2)\(^{ab}\) | \( H = 9.5; \ p \leq 0.05 \) |
|                     | *Solidago canadensis*   | 4.1 (±0.1)\(^{ab}\) | \( H = 9.5; \ p \leq 0.05 \) |
|                     | *Solidago virgaurea*    | 5.1 (±0.5)\(^{b}\)  | \( H = 7.3^{ns} \) |
|                     | *Solidago gigantea*     | 3.8 (±0.5)\(^{a}\)  | \( H = 7.3^{ns} \) |
| Fruits with removed pappus | *Solidago ×niederederi* | 3.6 (±0.3) | \( H = 7.3^{ns} \) |
|                     | *Solidago canadensis*   | 4.2 (±0.6) | \( H = 7.3^{ns} \) |
|                     | *Solidago virgaurea*    | 4.4 (±0.3) | \( H = 7.3^{ns} \) |
|                     | *Solidago gigantea*     | 3.8 (±0.1) | \( H = 7.3^{ns} \) |

The diverse letters in superscript indicate the significant differences between the taxa.

**Table 6** Differences in the mean values (±SD) of coefficient of velocity between *Solidago ×niederederi*, *S. canadensis*, *S. virgaurea*, and *S. gigantea*, in the groups of fruits with intact and removed pappus, on the basis of four replicates of 50 fruits

| Experimental group | Taxon                  | Coefficient of velocity | Statistical significance level (Kruskal-Wallis H test) |
|--------------------|------------------------|-------------------------|-------------------------------------------------------|
| Fruits with intact pappus | *Solidago ×niederederi* | 25.2 (±1.2)\(^{ab}\) | \( H = 9.5; \ p \leq 0.05 \) |
|                     | *Solidago canadensis*   | 23.0 (±2.1)\(^{ab}\) | \( H = 9.5; \ p \leq 0.05 \) |
|                     | *Solidago virgaurea*    | 19.8 (±11.7)\(^{a}\) | \( H = 7.2^{ns} \) |
|                     | *Solidago gigantea*     | 26.6 (±3.6)\(^{b}\)  | \( H = 7.2^{ns} \) |
| Fruits with removed pappus | *Solidago ×niederederi* | 27.8 (±2.3) | \( H = 7.2^{ns} \) |
|                     | *Solidago canadensis*   | 24.3 (±3.3) | \( H = 7.2^{ns} \) |
|                     | *Solidago virgaurea*    | 22.9 (±1.2) | \( H = 7.2^{ns} \) |
|                     | *Solidago gigantea*     | 26.1 (±0.7) | \( H = 7.2^{ns} \) |

The diverse letters in superscript indicate the significant differences between the taxa.

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but it differed significantly from its parental species (Table 2). Moreover, there were significant differences between the studied taxa in the length of cypsela (Table 2). On the other hand, the width of cypsela in the hybrid was similar to that observed in *S. canadensis* and *S. gigantea* (Table 2).

*S. virgaurea* had the greatest number of pappus bristles, the longest pappus bristles and the largest size of cypselae, whereas the lowest number of pappus bristles, the shortest pappus bristles and the smallest size of the cypselae were found in *S. canadensis* (Table 2).

**Seed germination test results**

In both experimental groups (fruits with intact pappus and fruits with removed pappus), there were significant differences between the hybrid, parental species and *Solidago gigantea* in the final percentage of germinated seeds (Table 3) and Timson’s index (Table 4). However, considering the mean germination time (Table 5) and the coefficient of velocity (Table 6) the significant differences between the taxa were found only in the group of fruits with intact pappus. In the group of fruits with intact pappus, the highest and the lowest percentage of germinated seeds was achieved by *S. gigantea* and *S. canadensis*, respectively, whereas in the group of fruits with removed pappus, it was achieved by *S. virgaurea* and *S. canadensis*, respectively (Table 3).

Moreover, in the group of fruits with intact pappus, the fastest seed germination was noticed in *S. gigantea* (Tables 4, 5 and 6), whereas the slowest seed germination occurred in *S. virgaurea* (Tables 4, 5 and 6). In the group of fruits with removed pappus, the fastest and the slowest seed germination occurred in *S. virgaurea* and *S. canadensis*, respectively (Table 4). According to the Mann-Whitney U test results, the studied taxa showed the differences in germination parameters between the groups of fruits with intact and removed pappus. The final percentage of germinated seeds was remarkably greater in the group of fruits with intact pappus than in the group of fruits without the pappus in *S. canadensis* (*p* ≤ 0.05) and *S. gigantea* (*p* ≤ 0.05), whereas in *S. ×niederederi* and *S. virgaurea* it did not differ between the two experimental groups (Table 7). In *S. virgaurea*, fruits with intact pappus presented the significantly lower value of Timson’s index than the fruits without the pappus

**Table 7** Differences in the mean values (±SD) of final percentage of germinated seeds between the groups of fruits with intact and removed pappus in *Solidago ×niederederi*, *S. canadensis*, *S. virgaurea*, and *S. gigantea*, on the basis of four replicates of 50 fruits

| Taxon                | Experimental group (A – fruits with intact pappus, B – fruits with removed pappus) | Final percentage of germinated seeds | Statistical significance level (Mann-Whitney U test) |
|----------------------|-----------------------------------------------------------------------------------|-------------------------------------|-----------------------------------------------------|
| *Solidago ×niederederi* |                                                                                   |                                     |                                                     |
| A                    | 67.0 (±5.0)                                                                        | U = 7.0;                            |                                                     |
| B                    | 64.5 (±9.3)                                                                        | *p* = 0.88                          |                                                     |
| *Solidago canadensis* |                                                                                   |                                     |                                                     |
| A                    | 60.0 (±2.8)                                                                        | U = 0.5;                            |                                                     |
| B                    | 47.5 (±1.9)                                                                        | *p* ≤ 0.05                          |                                                     |
| *Solidago virgaurea*  |                                                                                   |                                     |                                                     |
| A                    | 71.0 (±5.0)                                                                        | U = 3.0;                            |                                                     |
| B                    | 82.0 (±9.1)                                                                        | *p* = 0.19                          |                                                     |
| *Solidago gigantea*   |                                                                                   |                                     |                                                     |
| A                    | 91.0 (±3.5)                                                                        | U = 0.5;                            |                                                     |
| B                    | 68.5 (±7.2)                                                                        | *p* ≤ 0.05                          |                                                     |

**Table 8** Differences in the mean values (±SD) of Timson’s index between the groups of fruits with intact and removed pappus in *Solidago ×niederederi*, *S. canadensis*, *S. virgaurea*, and *S. gigantea*, on the basis of four replicates of 50 fruits

| Taxon                | Experimental group (A – fruits with intact pappus, B – fruits with removed pappus) | Timson’s index | Statistical significance level (Mann-Whitney U test) |
|----------------------|-----------------------------------------------------------------------------------|----------------|-----------------------------------------------------|
| *Solidago ×niederederi* |                                                                                   | 472.5 (±44.9) | U = 7.0;                                            |
| A                    | 473.0 (±50.2)                                                                     |               |                                                     |
| *Solidago canadensis* |                                                                                   | 411.0 (±17.6) | U = 0.5;                                            |
| A                    | 325.5 (±37.5)                                                                     | *p* ≤ 0.05    |                                                     |
| *Solidago virgaurea*  |                                                                                   | 418.5 (±8.5)  | U = 0.5;                                            |
| A                    | 544.0 (±50.4)                                                                     | *p* ≤ 0.05    |                                                     |
| *Solidago gigantea*   |                                                                                   | 650.5 (±40.4) | U = 0.5;                                            |
| A                    | 493.0 (±53.7)                                                                     | *p* ≤ 0.05    |                                                     |
The reversed trend was noticed in *S. canadensis* and *S. gigantea* (*p* ≤ 0.05), whilst fruits of *S. ×niederederi* showed similar values of Timson’s index in both groups (Table 8). Moreover, seeds of all the studied taxa showed similar values of mean germination time and coefficient of velocity in both experimental groups (Tables 9 and 10).

### Discussion

Based on the results, we can suggest that the length of cypsela is a useful morphological trait that allows distinguishing *Solidago ×niederederi* from its parental species and *S. gigantea*. Moreover, the number of pappus bristles appears to be an additional diagnostic character of *Solidago sect. Solidago* nothosubsect. *Triplidago* to which *S. ×niederederi* belongs (Gudžinskas and Žalneravičius 2016). However, this character should be also examined in *S. ×snarskisii* Gudžinskas and Žalneravičius, a hybrid between *S. gigantea* and *S. virgaurea*, which is the second known hybrid of the nothosubsection *Triplidago* (Gudžinskas and Žalneravičius 2016). Furthermore, our results showing differences in the length of fruits between *S. ×niederederi* and its parental species correspond to previously published data (Migdałek et al. 2014). Similarly, Gudžinskas and Žalneravičius (2016) evidenced significant differences in the length of pappus between *S. gigantea* and *S. virgaurea*.

Until now, seed germination of *S. ×niederederi* was tested using the fruits with intact pappus (Pliszko and Kostrakiewicz-Gierałt 2017a, 2017b, 2018a). In this study, we demonstrated that seed germination of the hybrid occurs in fruits with removed pappus as well. The hypothesis that the mechanical removal of pappus decreases the final percentage and speed of seed germination can be fully accepted in *S. canadensis* and *S. gigantea*, whereas in the case of *S. ×niederederi* and *S. virgaurea* it must be rejected. However, the significant differences in the speed of seed germination between two experimental groups in *S. canadensis* and *S. gigantea* were confirmed based on the Timson’s index only (Table 8). The results of statistical analysis of the mean germination time (Table 9) and coefficient of velocity (Table 10) suggested no effect of pappus removal on the speed of seed germination in all the studied taxa. Furthermore, it is

### Table 9 Differences in the mean values (±SD) of mean germination time between the groups of fruits with intact and removed pappus in *Solidago ×niederederi*, *S. canadensis*, *S. virgaurea*, and *S. gigantea*, on the basis of four replicates of 50 fruits

| Taxon                  | Experimental group (A – fruits with intact pappus, B – fruits with removed pappus) | Mean germination time | Statistical significance level (Mann-Whitney U test) |
|------------------------|-------------------------------------------------------------------------------------|----------------------|------------------------------------------------------|
| *Solidago ×niederederi*| A 4.0 (±0.2)                                                                         | U = 3.0; p = 0.19    |
|                        | B 3.6 (±0.3)                                                                         |                      |
| *Solidago canadensis*  | A 4.1 (±0.1)                                                                         | U = 8.0; p = 0.96    |
|                        | B 4.2 (±0.6)                                                                         |                      |
| *Solidago virgaurea*   | A 5.1 (±0.5)                                                                         | U = 1.0; p = 0.06    |
|                        | B 4.4 (±0.3)                                                                         |                      |
| *Solidago gigantea*    | A 3.8 (±0.5)                                                                         | U = 8.0; p = 0.96    |
|                        | B 3.8 (±0.1)                                                                         |                      |

### Table 10 Differences in the mean values (±SD) of coefficient of velocity between the groups of fruits with intact and removed pappus in *Solidago ×niederederi*, *S. canadensis*, *S. virgaurea*, and *S. gigantea*, on the basis of four replicates of 50 fruits

| Taxon                  | Experimental group (A – fruits with intact pappus, B – fruits with removed pappus) | Mean germination time | Statistical significance level (Mann-Whitney U test) |
|------------------------|-------------------------------------------------------------------------------------|----------------------|------------------------------------------------------|
| *Solidago ×niederederi*| A 25.2 (±1.2)                                                                        | U = 3.0; p = 0.19    |
|                        | B 27.8 (±2.3)                                                                        |                      |
| *Solidago canadensis*  | A 23.0 (±2.1)                                                                        | U = 6.0; p = 0.66    |
|                        | B 24.3 (±3.3)                                                                        |                      |
| *Solidago virgaurea*   | A 19.8 (±11.7)                                                                       | U = 1.0; p = 0.06    |
|                        | B 22.9 (±1.2)                                                                        |                      |
| *Solidago gigantea*    | A 26.6 (±3.6)                                                                        | U = 8.0; p = 0.96    |
|                        | B 26.1 (±0.7)                                                                        |                      |
worth mentioning that in other seed germination tests, in which the sand was used as a substrate (Pliszko and Kostrakiewicz-Gierańt 2017a, 2017b, 2018a), the percentage of germinated seeds of the hybrid was higher than that achieved on filter paper in this study. However, the percentage of germinated seeds could be also affected by genetic differences between the hybrid populations from which the fruits have been sampled. Moreover, it is hard to find a well-isolated population of S. ×niederederi in the wild and there is a possibility of backcrossing with one or both parental species. The influence of backcrossing on seed germination in the hybrid needs a separate study. In this paper, we focused on the effect of pappus removal on seed germination in relation to general fruit morphology and what is most important is that the hybrid is morphologically intermediate between its parental species (Table 2). At the same time, it is interesting to note that in some species of di- or trimorphic fruits the seed germination percentage is higher in fruits producing the pappus than in those without the pappus. It was observed inter alia in Garhadiolus papposus Boiss. & Buhse (Sun et al. 2009), Heterotheca subaxillaris var. subaxillaris (Lam.) Britton & Rusby (Baskin and Baskin 1976), Leontodon longirrostris (Finch & P.D. Sell) Talavera (de Clavijo 2001), L. saxatilis Lam. (Brändel 2007), Scorzonoides palisiae (Izuq.) Greuter & Talavera, and S. muelleri (Sch. Bip.) Greuter & Talavera (Cruz-Mazo et al. 2010).

Although the number of pappus bristles and the length of pappus bristle in S. ×niederederi and S. gigantea were similar (Table 2), the effect of pappus removal on the final percentage of seed germination in these two species was different (Table 7). We assumed that in species of bigger fruits like S. ×niederederi and S. virgaurea the removal of pappus did not decrease the percentage of germinated seeds as a result of dispersal strategy. During fruit dispersal, long pappus bristles seem to experience more damage than the short ones. In consequence, the loss of pappus bristles enhances the contact of the fruits with the soil and may increase the rate of seed germination. For example, in the case of Symphyopappus reticulatus Baker, if the thick and rigid bristles of the pappus did not separate from the cypselae during dispersal, contact with the substrate would be much more difficult (Marzinek and Oliveira 2010). On the other hand, small fruits could be more sensitive to pathogens after mechanical damage or loss of the pappus. The pappus damage in the effect of insect larvae feeding was observed in several taxa (e.g., Romero and Neto 2005; Winston et al. 2017) and the defensive role of pappus against the attack of herbivores was pointed out by Stuessy and Garver (1996), as well as Bohm and Stuessy (2001). Moreover, de la Peña and Bonte (2014) found that after exposure to aboveground herbivory, Taraxacum officinale produced seeds with longer pappus, increasing dispersal ability. The physiological mechanisms related to the effect of pappus removal on seed germination in Solidago should be explored in accordance with the micromorphology and anatomy of their fruits as it was performed in the case of Taraxacum officinale (Hale et al. 2010). Moreover, it would be worthwhile to test the involvement of twin hairs, which are found on the fruit surface of Solidago species, in fruit hydration and seed germination. Interestingly, De-Paula et al. (2015) proved that the twin hairs on the fruit surface of Emilia fosbergii Nicolson constitute the main passage for water intake, which is essential for seed imbibition and germination, and after imbibition, they release mucilage that can adhere the diaspore.

Production of numerous fruits, which are easily dispersed by wind, is one of the most important factors facilitating naturalization and invasion of S. canadensis and S. gigantea (e.g., Huang et al. 2007; Bohcenek et al. 2016). The successful establishment of S. ×niederederi also depends on fruit production (Pliszko and Kostrakiewicz-Gierańt 2017b). Similarly to native S. virgaurea, the loss of pappus bristles does not affect seed germination in the hybrid. What is more, after pappus removal, the percentage of seed germination in the hybrid is still relatively high (Table 2). The ability of seed germination after mechanical damage or loss of the pappus bristles seems to be beneficial for S. ×niederederi establishment since its seed set is usually limited (Migdalek et al. 2014).

**Conclusions**

Solidago ×niederederi differs from its parental species and S. gigantea in the length of cypselae. It appears that the small size of the cypselae could be responsible for the negative effect of pappus removal on seed germination. However, further investigations are needed to reveal the importance of pappus and other fruit structures in seed germination in Solidago species.

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**Compliance with ethical standards**

**Conflict of interest**

The authors declare that they have no conflict of interest.

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