Response of oriental xerophytes to the occidental industrial revolution

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Abstract

Since the Industrial Revolution, human activities have contributed substantially to climate change, by adding CO₂ to the atmosphere, especially since the mid-20th century (the “Great Acceleration”). Climatic change does not have the same impact on different regions of the Earth, neither in the recorded past, nor in models of the future. Therefore, to anticipate on these changes, we need to understand and be able to predict the possible responses of the different regional vegetations of the world to these changes, and most significantly to increased drought conditions. The aim of this study is to understand the response of the xerophytes of the immense oriental Irano-Turanian bioregion to post-industrial global warming and to compare it with the response of the xerophytes of the neighbouring occidental Mediterranean bioregion.

We measured stomata index and stomata density from 83 herbarium sheets (coll. 1821-2014) from species of the non-succulent xerophyte, *Haplophyllum*. We tested for differences before and after the “Great Acceleration” in both bioregions. SI decreased in the occidental species (significant only for abaxial leaf side), whereas SI significantly increased in the oriental species (both sides). We suggest that changes in both occidental and oriental species are linked to atmospheric CO₂ due to the different constraints that act on their growth. In light-limited occidental species, atmospheric CO₂ caused the stomata index decrease, whereas in the predominantly water-limited oriental species, increased drought stress and temperature (climatic change) caused stomata index increase. In conclusion, we propose that whereas atmospheric CO₂ directly caused a decrease in stomata index in occidental xerophytes, it indirectly caused an increase in stomata index in oriental xerophytes *via* climate change (increase in aridity, drought stress, and temperature). This study highlights the considerable potential of research based on historical herbarium collections to answer ecological questions, especially regarding climatic change.

**Keywords:** atmospheric CO₂, industrial revolution, Occident, Orient, xerophytes
1. Introduction

The Earth has experienced a constantly changing climate in the time since plants first evolved. Carbon dioxide (CO$_2$) is an important greenhouse gas and higher or lower atmospheric levels of CO$_2$ have been linked, respectively, to warmer or cooler climates in the past (Beerling and Chaloner, 1993; Crawley and Berner, 2001; Kürschner et al., 2001; van der Burgh et al., 1993). Over the period 1860-2017, the global atmospheric partial pressure of CO$_2$ increased from 280 to 407.39 ppm (figure 1a). Yearly CO$_2$ release has consistently increased over time, but strongly accelerated after WWII, an event called the “Great Acceleration” (Hibbard et al., 2006; McNeill and Engelke, 2016; Steffen et al., 2015); see Fig. 1b). As a consequence, the Earth surface temperature increased and more prolonged dry periods alternate with more intensive rainfall events (Bartholomeus et al., 2012; Solomon et al., 2007), thereby affecting vegetation characteristics (Bates et al., 2008; Wegehenkel, 2009).

Climatic change does not have the same impact on different regions of the Earth, neither in the recorded past, nor in models of the future (Pachauri et al., 2014). Biogeographic origins and constraints based on lineage may also influence the way plants respond to global change in the Anthropocene, including elevated CO$_2$, warming, and changes in rainfall (Cavender-Bares et al., 2016). Therefore, to anticipate on these changes, we need to understand and be able to predict the possible responses of the different regional vegetations of the world to these changes, and most significantly to increased drought conditions. At the broadest scale, the area of the Earth can be divided into distinct bioregions, also called floristic regions in plant sciences (Kreft and Jetz, 2010; Takhtajan, 1986).

Among floristic regions, the Irano-Turanian (IT) region is one of the largest: it occupies the vast drylands of Eurasia, covering ca. 30% the surface of the continent, from easternmost Mongolia to the Sinai Peninsula (Manafzadeh et al., 2016); Fig. 1c).

Unlike the Mediterranean region (i.e., Occident) which enjoys a mild Summer-dry climate (Takhtajan, 1986), the IT region (i.e., Orient) is characterised by high continentality, low winter temperature, and strong precipitation seasonality (Djamali et al., 2012). Given these climatic conditions, plants adapted to low-water availability, i.e., xerophytes are predominant. In contrast with the neighbouring Mediterranean floristic region where vegetation is dominated by forests and shrubland (maquis), trees are rare in the IT region, and geophytes and low shrubs are dominant (Takhtajan, 1986). Moreover, the largely industrial occidental countries (inside the Mediterranean
floristic region) and the mostly developing oriental countries (inside the IT floristic region) have both shown the great acceleration in increase of CO₂ emissions since the 1950 (figure 1b).

Despite their importance in the evolution of the Eurasian flora, the adaptation of the xerophytes of the immense IT region to post-industrial global warming has never been studied. Moreover, no study has yet investigated whether the responses of xerophytic elements to climatic change differ between the Mediterranean (occidental) and the Irano-Turanian (oriental) xerophytes.

The xerophytic genus *Haplophyllum* A. Juss. from the Citrus family (Rutaceae) is a characteristic genus of the IT floristic region (Takhtajan, 1986; Zohary, 1973) whose evolution is closely connected with the geological and climatic development of the arid and semi-arid areas of the IT region (Manafzadeh et al., 2014). *Haplophyllum*’s main centre of diversity lies in the IT region, but it is also present in the Mediterranean floristic region (figure 1c; (Salvo et al., 2011)). *Haplophyllum* comprises 68 species of perennial herbs and shrubs with elliptical to linear leaves, growing overwhelmingly in open, dry, sunny habitats, in steppe and semi-desert areas in the Orient and in open woodlands, maquis, and forests in the Occident (Salvo et al., 2011; Townsend, 1986). *Haplophyllum* is thus a perfect case study to understand the effect of post-industrial warming on Eurasian xerophytes.

Stomata are the microscopic structures on the epidermis of leaves formed by two specialized guard cells that control the exchange of water vapor and CO₂ between plants and the atmosphere (Willmer and Fricker, 1996). According to their water storing strategies, xerophytes have either relatively low stomatal density (SD: stomata number per surface unit) in succulent xerophytes, or relatively high SD in non-succulent xerophytes, as in *Haplophyllum* (Maximov, 1929; Volkens, 1887). CO₂ increase has been shown to mostly cause a decrease in SD (reviewed in (Royer, 2001)). Stomata density is easy to measure and is often used when epidermal cells cannot be counted accurately; however, SD can be affected both by the initiation of stomata and the expansion of epidermal cells, which in turn is a function of many variables (e.g., light, temperature, water status, position of leaf on crown, and intra-leaf position). Carbon dioxide plays a stronger role in stomatal initiation than in epidermal cell expansion; therefore Salisbury (Salisbury, 1927) introduced the stomatal index (SI), which normalizes for the effects of this expansion. The SI is
defined as the number of stomata per unit of leaf area divided by the number of epidermal cells plus number of stomata per unit leaf area (see equation below).

\[
SI (\%) = \frac{\text{stomata number}}{\text{surface unit}} \times 100
\]

The SI is considered to be fairly constant within the leaves of a single plant and exhibits a clear response (usually an increase) to increased atmospheric CO\(_2\) (Beerling and Royer, 2002; Greenwood et al., 2003; Retallack, 2001; Royer, 2001; Willmer and Fricker, 1996). Gas exchange usually takes place on the shaded underside of the leaf, the abaxial side, where stomata are more abundant and more uniformly distributed than the upper side of the leaf, the adaxial side, which can also be completely devoid of stomata. However, no significant difference in response between the two different sides of the leaves was found in experimental increases on atmospheric CO\(_2\) (Royer, 2001). We thus expect that post-industrial increase in CO\(_2\), especially after the great acceleration, should decrease SI and SD in both the occidental (Mediterranean) and oriental (IT) plants. We also expect that this CO\(_2\) increase leads to a stronger decrease in SI and SD in the abaxial than in the adaxial surface of the leaves. In order to assess the impact of CO\(_2\) increase on leaf parameters, we tested for differences between values of SI and SD on each leaf side before and after the great acceleration (the date of which we set at 1950).

We therefore studied herbarium collections of both historical and recent specimens of oriental (IT) and occidental (Mediterranean) xerophytes (i.e., \textit{Haplophyllum}), in order to answer the following questions: (i) what is the stomata response in Eurasian xerophytes (i.e., \textit{Haplophyllum}) to post-industrial increase of atmospheric CO\(_2\) concentration? and (ii) is this response dependant on floristic regions?

2. Material and methods

2.1. Taxon sampling

Two hundred and seventeen herbarium sheets from the herbarium of the Natural History Museum in Vienna (W) and from the Herbarium of the University of Zurich (Z) were sampled. Due to poor preservation state and the difficulties to remove cuticular waxes (see below) data acquisition was possible for 83 of the 217 specimens which were collected from 1821 to 2014. Our final dataset includes 16 species of \textit{Haplophyllum}, 12 of which occur in the Orient (inside the IT floristic region) and
three of which occur in the Occident (inside the Mediterranean floristic region). One species occurs in both the Orient and the Occident (table S1). The herbarium authorities did not allow us to destructively sample more than one leaf per sheet.

2.2. Data acquisition

The leaves were removed from the herbarium sheets with forceps, and were softened in a solution of sulfosuccinate for three days (Erbar, 1995). The medial portion of the leaf blade has been shown to display the most regular arrangement of stomata (especially on the abaxial side (Rowson, 1946; Sharma and Dunn, 1968, 1969). Thus, the medial portion of each leaf blade was dissected out, sonicated for 2.5h in xylene to remove cuticular waxes, critical point dried, mounted on scanning electron microscope stubs, and sputter-coated with gold. Imaging was carried out on a JEOL JSM 6390 SEM at 10 kV.

Stomata and epidermis cells were counted manually on a leaf surface of 0.0775 mm².

2.3. Data analysis

Tukey’s Honest Significance Difference test and Analyses of Variance (ANOVA) were implemented in R using the “MASS” and “car” packages on the SI and SD datasets to understand the change of these variables between Occident and Orient pre- and post- 1950.

3. Results

Table 1 and figure 2 summarise the results of the analyses of leaf traits (SI and SD) detailed in Supplementary file S1. Significant differences between pre- and post-1950 values of SI were identified for both leaf sides for both regions (Occident versus Orient), except for the occidental species on the adaxial leaf side. The stomata index significantly decreased in the occidental species (significant only for abaxial side), whereas a significant increase was observed in the oriental species (significant for both sides; see table 1 and figure 2a, b). Significant differences between pre- and post-1950 were not identified for changes in SD, except for oriental species on the abaxial side of the leaves (see table 1 and figure 2c, d).

4. Discussion

Plants respond to the environmental signals they perceive by changes in their phenotype to increase individual fitness (Trewavas, 2009). The most conspicuous post-industrial environmental change that induces adaptations in plant phenotypes is
the global increase in atmospheric CO$_2$ concentration (de Boer et al., 2011; Ellis, 2015; Xu et al., 2015). Our results indicate that SI decreased between pre- and post-1950 in the occidental *Haplophyllum* species (significant only for abaxial side; table 1, Fig. 2a, b), but significantly increased between pre- and post-1950 in the oriental *Haplophyllum* species on both sides of the leaves (table a, Fig. 2a, b). Values for SD exhibited no significant trend possibly due to adaptation to other environmental conditions and variation in leaf expansion (table 1, Fig. 2c, d; (Royer, 2001)).

The decrease in SI observed in occidental species of *Haplophyllum* corroborates the studies on herbarium and fossil material over the past decades that overwhelmingly indicate an inverse relationship of SI with atmospheric CO$_2$ concentration (e.g., Beerling and Chaloner, 1993; Royer, 2001). The increase in SI observed in oriental species of *Haplophyllum*, however, does not fit into this pattern. Other environmental factors must be responsible for this observation. Except CO$_2$, other environmental factors that have been shown to influence stomata initiation are: irradiance (Furukawa, 1998; Gay and Hurd, 1975; Schoch et al., 1980; Sharma and Dunn, 1968, 1969), temperature (Ferris et al., 1996; Salisbury, 1928; Salisbury, 1927; Wagner, 1998), and drought stress (Makbul et al., 2011; Salisbury, 1927). Increases in all abovementioned factors have been shown to increase SI. These factors are expected to affect the oriental and occidental species of *Haplophyllum* differently because they grow in different climates and habitats: the occidental species grow in the mild Mediterranean climate under tree cover, whereas the oriental species of *Haplophyllum* grow in the harsh IT climate, which is characterised by strong continentality (Djamali et al., 2012), and a scarcity of trees (Takhtajan, 1986).

Total solar irradiance has increased during the period 1800-present (Solanki et al., 2013); this increase is expected to especially affect cloudless arid regions. Our results support a stronger influence of irradiance on oriental species: the oriental species display notably higher SI values for the sun-exposed, adaxial side of their leaves compared to their Mediterranean counterparts (Fig. 2b), whereas on the shaded, abaxial side of the leaves no such differences can be found (Fig. 2a). This notwithstanding, evidence of the positive effect of irradiance on SI was based on depletion experiments where the plants were exposed to a fraction of normal sunlight where a decrease of 94% and 99% in irradiance caused a 1.6x (Furukawa, 1998) and 1.5x (Sharma and Dunn, 1969) reduction in SI, respectively. Given that (1) the relationship between percent of total sunlight and SI is linear (Furukawa, 1998), and
the average increases (pre to post 1950) in SI of oriental species of *Haplophyllum*
are 1.14x for abaxial side and 1.22x for adaxial side (table S1), our observations
would require increases in total sun irradiance of 20% and 45% respectively. These
differences in irradiance are two orders of magnitude higher than the percentual
increase in irradiance reconstructed by the least conservative model reviewed by
(Solanki et al., 2013), which proposes a 0.4% increase in irradiance since 1800
(Shapiro et al., 2011). Therefore, increases in irradiance do not appear to underlie the
observed increase in SI since pre-industrial times, although experimental confirmation
would be needed to test this.

Non-succulent xerophytes, such as *Haplophyllum* have been shown to possess
increased SI with small stomata as an adaptation to rapidly changing water
availability (Franks et al., 2009) and possibly also as an adaptation for the increased
need for leaf cooling (Porporato et al., 2001). Therefore, increase in aridity, drought
stress -a type of extreme events, whose frequency influence plants more than mean
changes (Reyer et al., 2013)- and temperature, such as occurred in the Occident and
Orient post-industrial revolution ((Hartmann et al., 2013), p208-222), would be
expected to increase SI further. However, oriental (IT) and occidental (Mediterranean) plants do not grow under the same constraints. In the harsh,
continental conditions that the oriental *Haplophyllum* species experience, plant
growth models derived from long-term climate statistics (Nemani et al., 2003) predict
that plant growth is mostly water and secondarily temperature limited, whereas the
same models predict that the growth of their occidental counterparts are
predominantly sunlight limited (Allen et al., 2010; Boisvenue and Running, 2006;
Nemani et al., 2003; Running et al., 2004). Therefore the post-industrial increases in
aridity, drought stress, and temperature that occurred both in the Mediterranean and
IT regions ((Hartmann et al., 2013), p208-222) should have a stronger impact on the
SI of plants whose growth is already water- and temperature-limited. The
environment may thus constrain SI more tightly than atmospheric CO₂, and
paradoxically, a decrease in SI allowed by higher atmospheric CO₂ would probably
not be advantageous to the plants due to constraints of water stress response and leaf
cooling.

In conclusion, we suggest that whereas atmospheric CO₂ directly caused a decrease in
SI in occidental xerophytes, it indirectly caused an increase in SI in oriental
xerophytes *via* climate change (increase in aridity, drought stress, and temperature).
Potential evapotranspiration will increase with rising temperatures, and this will probably make the world effectively drier in many areas, independently of changes in precipitations (Cavender-Bares et al., 2016). Moreover, climate models project that arid and semiarid midlatitudes will become even drier than at present (Collins et al., 2013). Thus, in the future water stress will likely increase for all Eurasian xerophytes. Additional studies of the interaction between increased aridity and elevated CO₂ are needed to enable us to better understand and predict not only the responses to climate change of the xerophytes from the Mediterranean and IT regions, but of global dryland as well (Maestre et al., 2016).

Finally, this study also highlights the value of historical collections to answer ecological questions, especially regarding climatic change. By drawing on collections from several herbaria, made over two centuries, we show how these data may provide valuable information even of poorly studied areas (e.g., IT floristic region), and we highlight the increasing value of natural history collections in understanding long-term changes (Pyke and Ehrlich, 2010).

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Figure captions

**Figure 1.** CO$_2$ versus time and region. (a) Atmospheric CO$_2$ since the XVIII$^{th}$ century from ice core data and MaunaLoa observatory (modified from Scripps Institution of Oceanography http://bluemoon.ucsd.edu/co2_400/co2_800k_zoom.png). (b) CO$_2$ emission for selected countries from Occident (inside Mediterranean floristic region) and Orient (inside Irano-Turanian floristic region; data from (Boden and Andres, 2017)). (c) *Haplophyllum* in the Orient and Occident. *Haplophyllum* distribution, hatched; IT region, yellow; Mediterranean region, blue; Saharo-Arabian region, violet; Sudano-Zambesian region, brown (modified from (Manafzadeh et al., 2014)).

**Figure 2.** Stomata of *Haplophyllum*. Boxplots of values of SI and SD before and after 1950, in Orient and in Occident. (a) SI values on the abaxial side of leaves. (b) SI values on the adaxial side of leaves. (c) SD values on the abaxial side of leaves. (d) SD values on the adaxial side of leaves. Background figure is *Haplophyllum villosum*, modified from (Townsend, 1986).

Table captions

**Table 1.** Summary of results of ANOVA on significance and sign of differences between SI and SD of both leaf sides before and after 1950, for Occident and Orient.

**Table S1.** Dataset from 83 herbarium specimen of *Haplophyllum*. Stomata index and stomata density data from both leaf side, for 16 species, classified by region (Orient and Occident), and collection date (1821-2014). SI is obtained by the number of stomata per unit of leaf area divided to the number of epidermal cells plus number of stomata per unit leaf area; SD is obtained on a leaf surface of 0.0775 mm$^2$. 
### Table 1

| Stomata trait            | Difference | P value | Significance |
|--------------------------|------------|---------|--------------|
| **Abaxial Stomata Index** |            |         |              |
| Occident after 1950 - Occident before 1950 | -4.6 | 0.003 | **** |
| Orient after 1950 - Orient before 1950 | 2.9 | 0.003 | **** |
| **Adaxial Stomata Index** |            |         |              |
| Occident after 1950 - Occident before 1950 | -1.7 | 0.437 |          |
| Orient after 1950 - Orient before 1950 | 2.4 | 0.007 | **** |
| **Abaxial Stomata Density** |            |         |              |
| Occident after 1950 - Occident before 1950 | -9.7 | 0.985 |          |
| Orient after 1950 - Orient before 1950 | 51.1 | 0.028 | *          |
| **Adaxial Stomata Density** |            |         |              |
| Occident after 1950 - Occident before 1950 | 3.6 | 0.999 |          |
| Orient after 1950 - Orient before 1950 | 38.1 | 0.07 |          |

### Table S1

| Species     | Year | Region | Abaxial Stomata Index | Abaxial Stomata Index | Abaxial Stomata Density | Abaxial Stomata Density |
|-------------|------|--------|------------------------|------------------------|-------------------------|-------------------------|
| **patavinum** | 1821 | Occident | 25,23                  | 9,09                   | 348,39                  | 154,84                  |
| **linifolium** | 1829 | Occident | 18,37                  | 12                     | 116,13                  | 77,42                   |
| **buxbaumii** | 1836 | Orient  | 18,79                  | 15,79                  | 400                     | 348,3                   |
| **villosum** | 1839 | Orient  | 10,95                  | 8,57                   | 206,45                  | 193,55                  |
| **acutifolium** | 1843 | Orient  | 10,95                  | 9,24                   | 141,93                  | 193,55                  |
| **tenue** | 1847 | Orient  | 20                     | 18,3                   | 193,55                  | 167,74                  |
| **linifolium** | 1848 | Occident | 18,84                  | 13,33                  | 167,74                  | 103,22                  |
| **acutifolium** | 1849 | Orient  | 11,5                   | 10,71                  | 154,84                  | 167,74                  |
| **linifolium** | 1852 | Occident | 15,15                  | 12,5                   | 129,03                  | 103,22                  |
| **suaveolens Orient** | 1855 | Orient  | 16,36                  | 14,02                  | 232,26                  | 193,55                  |
| **suaveolens Orient** | 1859 | Orient  | 17,2                   | 13,29                  | 348,05                  | 296,49                  |
| **griffithianum** | 1861 | Orient  | 20                     | 20,88                  | 206,45                  | 245,16                  |
| **erythraeum** | 1861 | Orient  | 19,3                   | 20                     | 283,87                  | 335,48                  |
| **buxbaumii** | 1867 | Orient  | 18,6                   | 11,6                   | 412,9                   | 270,97                  |
| **patavinum** | 1868 | Occident | 18,62                  | 10,77                  | 245,16                  | 90,32                   |
| **suaveolens Occident** | 1877 | Occident | 15,25                  | 11,93                  | 232,26                  | 167,74                  |
| **acutifolium** | 1882 | Orient  | 13,64                  | 10,48                  | 232,26                  | 167,74                  |
| **linifolium** | 1890 | Occident | 15,79                  | 11,86                  | 116,13                  | 90,32                   |
| **linifolium** | 1891 | Occident | 16,05                  | 12                     | 167,74                  | 77,42                   |
| **suaveolens Occident** | 1892 | Occident | 13,38                  | 11,76                  | 219,15                  | 154,69                  |
| **thesioideae** | 1892 | Orient  | 5,63                   | 9,73                   | 103,22                  | 141,93                  |
| **tuberculatum** | 1893 | Orient  | 12,7                   | 18                     | 206,45                  | 232,26                  |
| **coronatum** | 1893 | Occident | 29,63                  | 14,38                  | 412,51                  | 270,97                  |
| **armenium** | 1894 | Orient  | 17,14                  | 12,09                  | 309,68                  | 283,87                  |
| **pilosum** | 1897 | Orient  | 15,49                  | 13,04                  | 283,6                   | 270,71                  |
| **pilosum** | 1898 | Orient  | 17,43                  | 15,79                  | 244,93                  | 348,05                  |
| **versicolor** | 1900 | Orient  | 11,76                  | 17,43                  | 154,69                  | 244,93                  |
| **thesioideae** | 1900 | Orient  | 10,53                  | 14,61                  | 206,45                  | 167,58                  |
| **acutifolium** | 1900 | Orient  | 12,09                  | 10,26                  | 141,93                  | 103,22                  |
| **Obtusifolium** | 1900 | Orient  | 6,48                   | 10,2                   | 90,32                   | 128,91                  |
| **versicolor** | 1902 | Orient  | 13,33                  | 19,95                  | 206,45                  | 245,16                  |
| **suaveolens Orient** | 1906 | Orient  | 14,61                  | 11,29                  | 258,06                  | 180,64                  |
| **suaveolens Occident** | 1907 | Occident | 13,33                  | 10,26                  | 206,45                  | 206,45                  |
| **linifolium** | 1907 | Occident | 15                     | 15                     | 154,84                  | 154,84                  |
| Name            | Year | Region  | Length | Width | Height | Width | Length | Width | Height | Width | Length |
|-----------------|------|---------|--------|-------|--------|-------|--------|-------|--------|-------|--------|
| *linifolium*    | 1912 | Occident| 12.33  | 10.34 | 116.13 | 154.84|        |       |        |       |        |
| *amnenum*       | 1914 | Orient  | 21.31  | 15.6  | 335.48 | 219.35|        |       |        |       |        |
| *erythraeum*    | 1935 | Orient  | 17.99  | 22.22 | 245.16 | 206.25|        |       |        |       |        |
| *coronatum*     | 1936 | Occident| 23.53  | 20    | 464.52 | 258.06|        |       |        |       |        |
| *versicolor*    | 1937 | Orient  | 17.97  | 19.58 | 296.77 | 361.29|        |       |        |       |        |
| *linifolium*    | 1944 | Occident| 11.11  | 11.11 | 167.58 | 128.91|        |       |        |       |        |
| *griffithianum* | 1949 | Orient  | 11.11  | 15.94 | 193.36 | 283.6 |        |       |        |       |        |
| *pilosum*       | 1964 | Orient  | 20.48  | 16.17 | 438.29 | 348.05|        |       |        |       |        |
| *linifolium*    | 1965 | Orient  | 11.45  | 19.03 | 193.55 | NA    |        |       |        |       |        |
| *erythraeum*    | 1967 | Orient  | 15.15  | 22.39 | 128.91 | 193.36|        |       |        |       |        |
| *coronatum*     | 1969 | Occident| 19.23  | 17.74 | 258.06 | 283.87|        |       |        |       |        |
| *thesioides*    | 1970 | Orient  | 11.54  | 16.67 | 232.26 | 219.35|        |       |        |       |        |
| *suaveolens Occident* | 1971 | Occident| 12.28  | 10.89 | 180.47 | 141.8 |        |       |        |       |        |
| *griffithianum* | 1971 | Orient  | 6.71   | 12.41 | 141.93 | 219.15|        |       |        |       |        |
| *patavinum*     | 1975 | Occident| 16.75  | 9.84  | 386.73 | 154.69|        |       |        |       |        |
| *obtusifolium*  | 1976 | Orient  | 5.98   | 14.38 | 90.24  | 270.71|        |       |        |       |        |
| *versicolor*    | 1977 | Orient  | 17.07  | 20    | 180.64 | 232.26|        |       |        |       |        |
| *thesioides*    | 1977 | Orient  | 10.87  | 13.33 | 193.55 | 258.06|        |       |        |       |        |
| *Suaveolens Orient* | 1977 | Orient  | 12.28  | 8.63  | 180.64 | 154.84|        |       |        |       |        |
| *thesioides*    | 1978 | Orient  | 13.82  | 13.95 | 219.35 | 232.26|        |       |        |       |        |
| *amnenum*       | 1981 | Orient  | 25.33  | 17.95 | 244.93 | 180.47|        |       |        |       |        |
| *tuberculatum*  | 1987 | Orient  | 15.66  | NA    | 335.48 | 412.9 |        |       |        |       |        |
| *patavinum*     | 1999 | Occident| 16.27  | 8.4   | 438.29 | 141.8 |        |       |        |       |        |
| *versicolor*    | 1999 | Orient  | 19.15  | 20.93 | 348.39 | 348.39|        |       |        |       |        |
| *patavinum*     | 2000 | Occident| 15.25  | 7.22  | 232.04 | 90.24 |        |       |        |       |        |
| *tuberculatum*  | 2000 | Orient  | 15.14  | 19.71 | 425.4  | 348.05|        |       |        |       |        |
| *coronatum*     | 2000 | Occident| 16.08  | 15.66 | 296.77 | 335.48|        |       |        |       |        |
| *suaveolens Occident* | 2001 | Occident| 9.77   | 7.09  | 167.58 | 116.02|        |       |        |       |        |
| *tuberculatum*  | 2001 | Orient  | 15.12  | 15.79 | 335.48 | 348.39|        |       |        |       |        |
| *suaveolens Occident* | 2004 | Occident| 8.79   | 7.22  | 103.13 | 90.24 |        |       |        |       |        |
| *tenue*         | 2004 | Orient  | 14.66  | 12.5  | 283.87 | 258.07|        |       |        |       |        |
| *villosum*      | 2007 | Orient  | 21.13  | 18.28 | 193.36 | 219.15|        |       |        |       |        |
| *villosum*      | 2007 | Orient  | 21.95  | 18.07 | 232.04 | 193.36|        |       |        |       |        |
| *pilosum*       | 2008 | Orient  | 26.83  | 21.05 | 283.6  | 206.25|        |       |        |       |        |
| *obtusifolium*  | 2008 | Orient  | 15.79  | 16.05 | 193.36 | 167.58|        |       |        |       |        |
| *pilosum*       | 2008 | Orient  | 25.69  | 17.7  | 361.29 | 258.06|        |       |        |       |        |
| *acutifolium*   | 2008 | Orient  | 16.28  | 15.15 | 180.47 | 128.91|        |       |        |       |        |
| *versicolor*    | 2008 | Orient  | 18.95  | 26.31 | 374.19 | 386.73|        |       |        |       |        |
| *villosum*      | 2008 | Orient  | 20.45  | 13.97 | 348.39 | 245.16|        |       |        |       |        |
| *tuberculatum*  | 2011 | Orient  | 18     | 19.3  | 554.84 | 283.87|        |       |        |       |        |
| *thesioides*    | 2011 | Orient  | 15.38  | 17.86 | 206.25 | 257.82|        |       |        |       |        |
| *buxbaumii*     | 2012 | Orient  | 20.53  | 18.37 | 399.62 | 464.07|        |       |        |       |        |
| *thesioides*    | 2012 | Orient  | 15.15  | 17.24 | 128.91 | 193.36|        |       |        |       |        |
| *villosum*      | 2013 | Orient  | 20     | 11.11 | 193.36 | 128.91|        |       |        |       |        |
| *amnenum*       | 2013 | Orient  | 27.66  | 26.88 | 355.16 | 322.7 |        |       |        |       |        |
| *suaveolens Orient* | 2013 | Orient  | 18.37  | 17.39 | 232.04 | 206.25|        |       |        |       |        |
| *linifolium*    | 2013 | Occident| 11.86  | 8.33  | 90.32  | 77.34 |        |       |        |       |        |
| *tuberculatum*  | 2014 | Orient  | 17.51  | 18.92 | 359.7  | 541.42|        |       |        |       |        |
| *suaveolens Orient* | 2014 | Orient  | 19.46  | 12.5  | 373.84 | 257.82|        |       |        |       |        |
