

1 **Research-in-context**

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3 **A willow drawing from 1786: the earliest depiction of intraspecific trait variation in**
4 **plants?**

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18 **Keywords**

19 intraspecific trait variation, leaf morphology, altitude, elevation, phenotypic plasticity,
20 environmental conditions, natural population, *Spix* sp., *Gentiana* sp., Bavarian Alps, Goethe,
21 history

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23 **Running title**

24 An early depiction of ITV

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1 **Abstract**

2 **Background and Aims**

3 The study of intraspecific trait variation (ITV) in plants has a long history, dating back to the
4 4th century BC. Its existence was widely acknowledged by the end of the 18th century,
5 although systematic and experimental studies commenced only a century later. However, the
6 historiography of ITV has many gaps, especially with regards to early observations and
7 visual documents. This note is a contribution to fill that gap.

8

9 **Methods**

10 The botanical works of Johann Wolfgang von Goethe (1749-1832), a German writer and
11 naturalist, were subjected to close reading. This included all publications and unpublished
12 sources related to botany between 1785 and 1832 (e.g. notes, drafts, diaries, letters,
13 drawings). This material is accessible in the multi-volume historical-critical edition of
14 Goethe's studies in natural science ("Leopoldina-Ausgabe").

15

16 **Key Results**

17 A diary entry from 9 September 1786 described changes in leaf morphology along an
18 elevation gradient in the Bavarian Alps. The leaves of an unidentified species of willow (*Spix*
19 *sp.*) and gentian (*Gentiana sp.*), respectively, were said to become narrower with increasing
20 elevation; leaves also stood further apart on twigs, and the latter became thinner. A crude
21 drawing of two willow twigs illustrated the differences. Goethe conjectured that the
22 differences were due to environmental conditions.

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1 **Conclusions**

2 Goethe's notes were anecdotal, and it is unclear whether the observed plant individuals
3 actually belonged to the same species. Nevertheless, the notes represent an early and clear
4 articulation of the hypothesis that changes to environmental conditions can cause ITV in a
5 natural plant population. The drawing may be the earliest visual record of environmentally-
6 mediated plant ITV in the wild.

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2 **A willow drawing from 1786: the earliest depiction of intraspecific trait variation in**
3 **plants?**

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5 In September 1786, a stagecoach wound its way up the Alpine foothills south of Munich. As
6 the coach climbed higher into the mountains, one of the passengers noticed changes in the
7 leaves and twigs of willows and gentians. The passenger was Johann Wolfgang von Goethe
8 (1749-1832), a celebrated German novelist with an emerging passion for botany. Goethe
9 eventually became a founding figure of plant morphology (Kaplan, 2001), mostly associated
10 with the foliar theory of the flower (Glover, 2014) and heteroblasty (Chitwood, 2014). But
11 here, in the foothills of the Bavarian Alps and at the beginning of both his botanical
12 endeavours and his journey to Italy, Goethe (1786) conjectured that changes to
13 environmental conditions might cause morphological variations within a plant species: “I
14 want to state an opinion about the influence of barometric altitude on plants, which needs
15 to be scrutinized. The more elastic air affects the organs of the plant, endowing it with the
16 utmost expansion and renders its existence more perfect. If there is enough moisture that
17 can enter the expanded organ, then the plant is well nourished and can develop best, grow
18 stronger and reproduce more. This thought occurred to me when I saw that a willow and
19 gentian were very fragile and had much space from node to node. They were formed as in
20 fig. 2 rather than as in fig. 1.”

21

22 [figs 1 and 2]

23

24 Goethe’s drawing depicted twigs of an unidentified willow (*Spix* sp.), not a gentian, as
25 is evident from the alternate arrangement of leaves and their lanceolate shape. Three

1 decades later, Goethe (1816-17) re-described the twigs in more detail: “While in the lower
2 regions branches and stalks were stronger and more sappy, the buds stood closer together,
3 and the leaves broader; the higher you got on the mountains the stalks and branches
4 became more fragile, the buds were at greater intervals, and the leaves thinner and more
5 lanceolate.” He explained the differences with “the influence which the altitude of the
6 mountain region evidently had on plants”. In effect, Goethe hypothesized that the
7 morphological differences in willows were an instance of environmentally-mediated
8 intraspecific trait variation (ITV) in a natural plant population. He may well have been
9 mistaken, of course. He failed to identify the species and simply insisted that “it was not a
10 case of different species”. Furthermore, even if the variation was intraspecific, the
11 environmental effects may have been mediated by phenotypic plasticity, genetic
12 differentiation, or both. Still, Goethe’s observation is noteworthy as a hypothesis about ITV,
13 and because the accompanying sketch may be the earliest visual record of an instance of
14 environmentally-mediated ITV in the wild.

15 Yet, neither Goethe’s unpublished observation nor his later public endorsements of
16 ITV (e.g. Agrawal, 2020) had discernible effects on subsequent authors. By the end of the
17 18th century botanists had already acknowledged the existence of ITV (Bowler, 2005). Linné,
18 for example, accepted that individuals of a given species may vary from one another if
19 subjected to breeding or exposed to different environmental conditions. The results were
20 “varieties” that belonged to one and the same “species”. In fact, the idea that
21 environmental differences may cause morphological differences within a species can be
22 traced back to antiquity. In the 4th century BC, Theophrastus remarked that “all those trees
23 which are common to both hill and plain are taller and finer in appearance when they grow
24 in the plain” (1916, p. 173). The dwarfing of plants at higher altitudes became a prime

1 example of environmentally-mediated ITV during the early and mid-19th century. It was
2 mentioned by naturalists such as Lamarck (Briggs & Walters, 1997), Humboldt & Bonpland
3 (1807, p. 109), and Darwin (1859, p. 45). Yet only in the 1890s did ITV emerge as an object
4 of sustained empirical inquiry. The transplant experiments of Gaston Bonnier and Anton
5 Kerner pioneered a new, experimental approach (Briggs & Walters, 1997). Today we know
6 that altitude can have major intraspecific effects on leaf morphology. Some of these effects
7 match Goethe's observations on *Spix* sp., others do not. For example, leaves tend to
8 become smaller with increasing altitude across many mountain areas and in many plant
9 species (e.g. Körner *et al.*, 1986); but leaves also tend to become wider, not narrower (e.g.
10 Flann *et al.*, 2002). Be that as it may, Goethe's sketch provides us with a unique glimpse into
11 the early history of research on intraspecific trait variation.

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15 references.

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1 **Figure caption**

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3 **Figures 1 and 2.** Twigs of a willow (*Spix* sp.) at low ('Fig. I') and high elevation ('Fig. II'). From

4 Goethe's *Tagebuch von der Reise nach Italien*, 9 September 1786 (LAI 9A, p. 339). Source:

5 Klassik Stiftung Weimar, Goethe- und Schiller Archiv/27/9.

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7 **[NB** The original figure consists of two parts, and the figure itself includes the labels 'Fig. I'

8 and 'Fig. II'. Since the figure is a historical document, the labels in the original figure should

9 be used. Hence, there is only one caption for both parts]