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Ecology and distribution of the Southeast Asian invasive liana Kudzu, *Pueraria lobata* (Fabaceae), in Southern Switzerland

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Pueraria lobata, Kudzu, is a perennial liana native in temperate to tropical East Asia. Introduced mainly as an ornamental plant into many (sub)tropical regions, and as a forage crop in the South-Eastern USA, it has spread vegetatively into adjacent forests and grasslands and has also been dispersed with garden waste. The objectives of this paper are: (i) to assess whether the ecology of *P. lobata* in Southern Switzerland is similar to that in the South-Eastern USA, where it causes great damage; (ii) to predict its further spread in Southern Switzerland. In Switzerland it already occurs in 32 sites covering 16 200 m^2; the shoots grow ≤ 26 cm per day and ≤ 11 m per year, forming ≤ 2 m thick mats. *P. lobata* infested sites contain about half as many plant species as similar sites without it. This paper shows that the ecology of *P. lobata* in Southern Switzerland is similar to that described for the USA. The broad climatic requirements of the species suggest that it could establish in many regions of Southern and Central Europe. However, it is not expected to spread on a large scale in Switzerland because there appears to be no establishment from seed and because its stands are always near settlements and thus mostly controlled.

Introduction

Kudzu, *Pueraria lobata* (Willd.) Ohwi, Fabaceae, is a perennial, semi-woody liana originating from temperate to tropical East Asia. It now occurs on all continents and is listed among the 'One Hundred of the World's Worst Invasive Alien Species' (ISSG, 2013). The species is on the EPPO A2 List of pests recommended for regulation and a Pest Risk Analysis is available for this species. For synonyms of *P. lobata* see GISD (2010). A description of the species is given in the methods section. The names of all the species are according to Lauber *et al.* (2012).

In the first half of the 20th century, *P. lobata* was widely introduced in the South-Eastern USA as an ornamental plant, as forage for livestock, as a soil cover to prevent erosion, and for soil improvement. Even culinary and healing qualities were mentioned (Shurtleff & Aoyagi, 1977). The species quickly spread and caused massive damage (Mitich, 2000; Blaustein, 2001; GISD, 2010). Therefore, in 1997, it was placed on the USA List of Federal Noxious Weeds (Forseth & Innis, 2004). In 2004, it covered some 3 million hectares in the USA and was spreading at a rate of over 50 000 ha per year (Forseth & Innis, 2004), causing enormous damage to agriculture, forestry, protected areas, wildlife, and outdoor sport activities as well as to power lines, roads and railway lines (Miller & Edwards, 1983; Forseth & Innis, 2004). Blaustein (2001) mentions a damage estimate of >500 million USD per year. Various control methods have been developed with differing levels of success (see EPPO, 2007 and GISD (Global Invasive Species Database), 2010).

In Western Europe, *P. lobata* is established in the northern Italian regions of Piedmont to Friuli-Venezia Giulia (Celesti-Grapow *et al.*, 2010). Arietti (1950) mentioned that, already in 1940, it occurred as an established alien near Brescia (Lombardy). Follak (2011) gives a map of the potential distribution and environmental threat of *P. lobata*; it ranges from Western France to Northern Italy, Austria and the former Yugoslavia. In Switzerland, it occurs only in Canton Ticino (one stand in adjacent Canton Grisons). For this region and in neighbouring Italy, *P. lobata* has been reported as an escaped garden plant already by Schröter (1956). At present, *P. lobata* has only caused minor problems in Switzerland (Infoflora, 2014).

The ecology of *P. lobata* has been widely studied in its native area (see e.g. Keung, 2002; Sun *et al.*, 2006; Heider *et al.*, 2007; GISD (Global Invasive Species Database), 2010), as well as in its introduced range in the USA (Duke, 1983; Miller & Edwards, 1983; Susko *et al.*, 1999; Mitich, 2000; Blaustein, 2001; Forseth & Innis, 2004; Jarnevich & Stohlgren, 2009; Coiner, 2012).

The first objective of this paper was to assess whether the ecology of *P. lobata* in Southern Switzerland is similar to that in the South-Eastern USA. The habitat of *P. lobata*

in the study region was characterised, and vegetation analyses of 19 stands were undertaken. Data on stem elongation rate is presented. The invasion by *P. lobata* in the USA led to a local decrease of native biodiversity, and ecosystem functions were disrupted (Mitich, 2000; Blaustein, 2001; Forseth & Innis, 2004; GISD (Global Invasive Species Database), 2010). To assess the extent to which this is also the case in Switzerland, the vegetation and soil pH of sites with *P. lobata* were compared with those of neighbouring ecologically similar sites where this species was absent.

The second objective of this paper was to assess whether *P. lobata* will spread in Southern Switzerland, and thus possibly lead to damage similar to that reported for the USA (see references above).

Methods

Description of *Pueraria lobata*

The following description summarizes information by Duke (1983), Miller & Edwards (1983), Mitich (2000), Blaustein (2001), Keung (2002), Weber (2003), Forseth & Innis (2004), EPPO (2007) and GISD (2010). *P. lobata* has herbaceous and ligneous stems that are only partially winter hardy. In the USA, they grow up to 30 cm per day and up to 30 m per year (Mitich, 2000), creeping on the soil or climbing trees to a height of 20 m. *P. lobata* has deciduous leaves and purple, sweetish smelling inflorescences grouped in 20 cm long racemes. The fruits are reddish-brown hairy legumes 4–10 cm in length containing 3–10 seeds. They are possibly dispersed by mammals and not thought to be spread by birds (Meisenburg & Fox, 2002). *P. lobata* almost exclusively spreads with runners and with garden waste; in both cases roots are formed at the nodes of the shoots, leading to new plants. The roots (with nitrogen fixing nodules) can reach a depth of 5 m; additionally, nutrient rich tubers of up to 180 kg are formed (Blaustein, 2001).

Locating and describing the stands

The database at www.infoflora.ch, the Swiss Centre for the Mapping of the Flora, was used to locate established stands of *P. lobata.*

The stand area was assessed with aerial photographs of Google Earth, except for those at Agno, Caslano, Croglio and Magliaso, where cadastral maps 1:1 000 could be obtained. The programme ArcGis 9 allowed the calculation of the areas. At each site, altitude, exposure, and coordinates were assessed, based on the maps at http://www.swissinfo-geo.org. Slope was measured with a clinometer, which was also used to assess the height of the trees covered with *P. lobata*. Interviews with the owners of *P. lobata* sites provided information about the management and the possible origin and age of the stands.

Requirements for meaningful comparisons of *P. lobata* sites with environmentally similar sites without this species

To be valid as 'natural experiments' (Diamond, 1983), the study sites were required to meet a clear requirement: that before invasion by *P. lobata*, the sites were the same as the uninfested control sites. A possibility for checking whether this requirement is fulfilled is to analyse the soils. Two soil profiles to a depth of 60 cm (fig 14 in Pron, 2006) and 14 to a depth of 20 cm, i.e. the main rooting zone of *P. lobata*, showed that the topsoils under this species and of those of the neighbouring environmentally similar plots without it were identical or at least very similar. A second possibility involves the growth pattern of *P. lobata*. If there is sufficient sunlight, as at all of the natural experiment sites of the present study, it was observed that *P. lobata* extends its runners in all directions, indicating that no special soil conditions are preferred by the young shoots that later form the stand. In summary, there is no reason to assume that the vegetative establishment of *P. lobata* only occurs under particular environmental conditions. Establishment by seeds has never been observed in Switzerland.

Vegetation analyses, and recording of flowering, seed production, establishment, and damaged leaves

Vegetation relevés, i.e. analyses according to the Braun-Blanquet-method described in Mueller-Dombois & Ellenberg (1974), were carried out in 19 homogeneous *P. lobata* stands of ≥ 50 m^2 (except for one of 30 m^2). In this method, the cover/abundance of every species present is denoted with numerical values: 5 corresponds to 75–100% cover; 4 to 50–75% cover; 3 to 25–50% cover; 2 to 5–25% cover or <5% cover but >50 individuals; 1 to 1–5% cover or < 1% cover but 6–50 individuals; + corresponds to <1% cover and ≤5 individuals; r corresponds to 1 individual with a cover of $\ll$ 1%. Values for species occurring in the same habitat but ≤ 1 m outside the relevé plot were placed in brackets. Following Mueller-Dombois & Ellenberg (1974), the average cover percentage of *P. lobata* was calculated as the average cover of the values mentioned above.

The vitality of fully developed plant individuals was determined by estimating their height. If it was less than one quarter of the average height described for the particular species by Lauber *et al.* (2012), the vitality was considered as reduced.

To assess the effect of *P. lobata* on plant species richness, vegetation relevés in stands with 100% *Pueraria* cover and in the nearest environmentally similar forest or mown stands (after 4–6 weeks regrowth) without this species were carried out, i.e. in the "natural experiment" design (Table 1). The similarity concerned altitude, exposure, slope, and soil. The distances (distance function in Google Earth) between the *P. lobata* sites and the respec-

Table 1. Number of plant species in plots with 100% cover of *Pueraria lobata*, and in neighbouring environmentally similar plots without this species. Data collected from 13 September to 9 October 2012

Site	Site Nr in Appendix	Plot size m^2	*P. lobata* 100% cover. Nr of spp.	No *P. lobata* i.e. forest. Nr of spp.	Distance between plot centres m
Unmanaged plots					
Magliaso	10	100	15	16	70
Colmegna 46° 1′ 19.78″ N 8° 45′ 7.48″E	IT*	100	13	21	70
Tronzano 46° 5′ 40.75″ N 8° 44′ 5.66″E	IT*	100	16	22	80
Sant'Abbondio	17	80	15	35	40
Ronco sopra Ascona	15	60	8	16	30
Maroggia 45°56′17.59″N 8°58′21.94″E	CH*	100	9	17	100
Locarno Monti della Trinità	9	100	3	10	40
Average ± SD			11.00 ± 4.51	19.57 ± 7.85	
Mown plots					
Counted 4–6 week after mowing; then the cover was 70 to 100%			*P. lobata stands with* 100% cover. Nr of spp.	Grassland without *P. lobata* Nr of spp.	
Caslano, mown 1×/year since 2005,	5	32	9	25	10
Cassina d'Agno, mown 4×/years since 2009	1	15	14	25	12
Average ± SD			11.50 ± 3.54	25.00 ± 0	

*Geographical coordinates given as not in Appendix 1.

tive forest sites were between 30 and 80 m (one was 100 m; Table 1). These distances were relatively large because the vegetation in the centres of the *P. lobata* stands (which were quite large in some cases) was compared with the vegetation of the nearest well-developed forests. In the mown stands, the plot area was 15 m^2, i.e. sufficient to include all the species present in the stand. In the forests, it was only 60–100 m^2 because no larger comparable sites could be found at <100 m from the respective *P. lobata* stands. This plot size is smaller than the so-called minimal area of 200–500 m^2 for forest relevés (Mueller-Dombois & Ellenberg, 1974). In larger forest plots one would probably have found a few additional species. However, the smaller relevé plots were sufficient for the present study because they yielded a clear pattern (Table 1). The number of species in Table 1 does not always correspond to that in the vegetation table in the Appendix 1, because in the former only the parts with the densest *P. lobata* cover were considered.

In 2006, 2011, and 2012, during approximately 40 visits to 32 sites in Southern Switzerland, it was examined whether the plants had flowers, seeds or damaged leaves, and whether young plants that might have developed from weed were present.

Measurement of shoot elongation and thickness of the *P. lobata* mats

Shoot elongation was measured for 10 shoots in Magliaso and for 14 in Caslano, i.e. in the largest and thus presumably oldest stands. Young shoots were marked at the third node in April 2006; subsequently, the increase in shoot length from this point was repeatedly measured every 5–10 days. Shoot elongation rate was calculated as the quotient between the shoot growth during the measuring period and the number of days of the latter. The data can be considered representative because, during the measuring period, the weather conditions showed no anomalies. The thickness of the *P. lobata* mats was measured in five well-developed stands (nr 1, 5, 10, 15, and 17 mentioned in the Appendix 1).

Measurement of soil pH

Eight cylindrical soil (sub)samples with ø 6 cm were taken at a depth of 1–6 cm (below the 10 cm thick layer of *P. lobata* litter) at the edge of 8 × 8 m plots situated at the centre of five stands of the study species. In the large, virtually impenetrable stands at Magliaso and Caslano, the soil samples were taken on transects of 10 m at 2 m inside the stand. Following the "natural experiment" design, the corresponding soil samples were taken in the nearest environmentally similar forests or grasslands with no *P. lobata* (Table 1). The eight subsamples of every site were mixed, air dried and sieved at 2 mm. Ten grams of this fine earth were mixed with 25 mL $CaCl_2$ (0.01 mol) and stirred; after ≥6 h, pH was measured with the pH Meter 744 of Metrohm, Herisau, Switzerland.

Statistical analyses

Comparisons of the plots with and without *P. lobata* were performed either with the paired t-test, if the pair-wise differences were normally distributed, or with the Wilcoxon signed rank test. The data given in the tables, figures, and text are averages with standard deviation.

Results

Description of the *Pueraria lobata* stands

As shown in the Appendix 1, the 19 stands are at an altitude of 210–400 m near Lakes Lugano and Maggiore. Slope was 10° to 80° (on rocks), mostly facing Southeast to Southwest. The area of the stands was 30–6500 m^2. Together with 13 additional stands (data at www.infoflora.ch), the total area is 16 200 m^2.

Since all stands were closer than 20 m to gardens, most of them probably originated from runners from individual plants in gardens or from garden waste. Only the stand near Magliaso (Fig. 1) was probably planted for erosion control. At the sites 1, 2, 8, 9, 10, 15 and 17, *P. lobata* climbed trees (at site 9 up to 22 m). It was observed that tall trees bend down and may partially break when they are covered with a mat of *P. lobata* and snow.

Fourteen stands were cut one or more times per year (at least in their borders), two were treated with herbicides, one was not managed at all, and for three stands no information was available (see Appendix 1).

Vegetation of the *Pueraria lobata* stands

The vegetation of the studied 19 stands varied widely in species number per relevé (6–24, average of 15) and species composition (see Appendix 1). The average cover of *P. lobata* was 55%; in 6 stands it was ≥75% (converted Braun-Blanquet values). A total of 97 vascular plant species were found, 46 of which occurred only once, often with reduced vitality compared to that in the *P. lobata* free surroundings. Most of the growth of the (other) species was in spring, before the *P. lobata* foliage was fully developed. Three species mentioned in Appendix 1 are on the Swiss Red List (Moser *et al.*, 2002) and locally threatened by being overgrown by *P. lobata*: *Cistus salviifolius* classified as VU (=vulnerable), *Celtis australis* as NT (=near threatened), and *Ornithogalum pyrenaicum* as NT. In total, 22 species (= 23%) listed in the Appendix 1 are neophytes (according to Moser *et al.*, 2002). Among these, the most invasive ones are *Ailanthus altissima*, *Erigeron annuus, Lonicera japonica, Phytolacca americana*, *Prunus laurocerasus,*, *Robinia pseudoacacia* and *Trachycarpus fortunei; they* occurred with frequencies between 26% and 58% in the vegetation table (Appendix 1). (Invasional meltdown was not assessed in the present study.)

Number of plant species in *Pueraria lobata* stands and in neighbouring environmentally similar stands without this species

Table 1 shows that in the unmanaged plots with 100% cover of *P. lobata* the average number of plant species was 11.0 ± 4.5; in the neighbouring, environmentally similar forest plots without *P. lobata* it was 19.6 ± 7.9. The large standard deviations are attributed to soil differences of the different pairs of plots. In unmanaged plots with a smaller cover percentage of *P. lobata*, the effects on species richness would, of course, have been smaller. For the plots mown once per year, the mean number of species in the *P. lobata* plot was 9 compared to 25 for the adjacent grassland plot without this species; the respective numbers for the plots mown four times per year were 14 and 25. Overall, the plots with 100% *P. lobata* cover contained significantly fewer species than the plots without this species (Wilcoxon signed rank test, $n = 9$; $P = 0.009$).

Fig. 1 *Pueraria lobata* covering the soil with a 2 m thick mat and climbing 15 m on trees of *Castanea sativa* and *Robinia pseudoacacia* near Magliaso (site 10, see details in Appendix 1).

Horizontal and vertical growth, flowering, seed production, establishment, and leaf damage

The average shoot elongation of well-established *P. lobata* plants ranged from 4 to 8 cm per day in June to 16 to 20 cm per day in July. The absolute maximum was 26 cm per day near Caslano at the end of June (data not shown). The overall average was 8.8 cm per day, yielding an average total shoot elongation of 11.3 m (21 April to 27 August 2006).

The thickness of the *P. lobata* mats in five well-developed stands was 1.5–2.0 m (average 1.8 m, see also Fig. 1).

Flowering was observed in ten well-established stands. In 2005, seeds were formed at the Caslano and Magliaso sites (5 and 10 in the Appendix 1), and in 2011 at two additional sites. No young plants that could have originated from seed were found in the over 40 surveys of *P. lobata* stands and their surrounding. Traces of animal feeding or signs of fungal or bacterial infections on green leaves were detected at only 5 of the 32 sites described at www.infoflora.ch. No evidence was found that animals spread the seeds.

Soils and soil pH

Pueraria lobata occurred on very different soils: from dolomitic lithosols to acidic brown-earths. Due to the enormous litter production of *P. lobata*, the topsoil contained clearly more organic matter than environmentally similar neighbouring soils without this species.

Figure 2 shows that the pH values of the topsoil under unmanaged or mown *P. lobata* stands varied between pH 4.8 and 7.1 (average 6.2 $\pm$ 0.9) and were higher (except at Caslano) by as much as 2.8 pH units than those of the neighbouring environmentally similar soils without this species (average 4.9 $\pm$ 1.2). With its enormous growth, *P. lobata* takes up large amounts of nutrient cations from deep soil horizon. With the litter, these ions accumulate in the topsoil and replace the H+ ion, what leads to a high pH because of the ion balance in the soil. In the dolomitic soils at Caslano, the concentration of Ca++ and Mg++ is so high, that they have similarly high pH values. The pH differences between the sites with and those without *P. lobata* are normally distributed; a paired t-test gave t = 3.72, $P = 0.01$.

Discussion

Situation in Switzerland

The data presented in this paper show that in Southern Switzerland, the stands of *P. lobata* vary considerably regarding slope, exposure, soil, size and cover. This is in agreement with findings of Sun *et al.* (2006) that, due to its deep and well-developed root system, *P. lobata* grows also on very dry sites and on nutrient poor soils. This is plausible, since the young plants developing at the shoot nodes obtain nutrients from roots and tubers that might be as much as 10 m away. After 3 years, the young plants become independent (GISD (Global Invasive Species Database), 2010). The large differences in the size of the stands

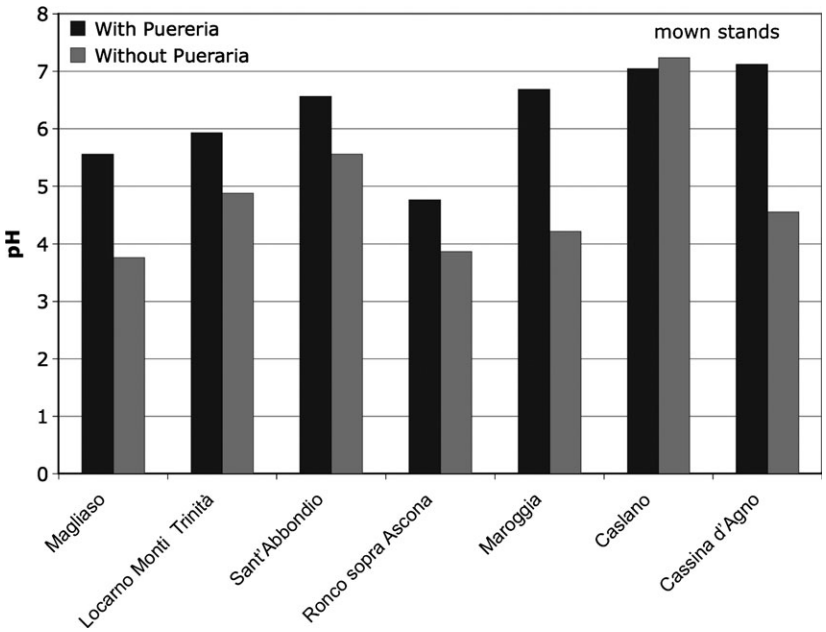

Fig. 2 Soil pH in the topsoil (mixture of 8 subsamples) under dense unmanaged *P. lobata* stands and in *P. lobata* free neighbouring environmentally similar forests or in mown *P. lobata* stands and adjacent *P. lobata* free grasslands mown at least once a year (details see Table 1 and Appendix 1). The main focus of the pH assessment was a comparison between the seven pairs of sites with and without *P. lobata*; therefore, the lack of error bars does not represent a major statistical fault.

(30–6500 m^2) and in the degree of *P. lobata* cover (15–100%) are related to their age and management. The top soils under *P. lobata* in Southern Switzerland had a pH ranging from 4.8 to 7.1 (average 6.2), which agrees with the pH range of 5.0–7.1 reported by Duke (1983) for the USA.

If the soils are such that the roots formed at the nodes of *P. lobata* can penetrate it, one can assume that in unmanaged sites, after 3–4 years, the cover of this species will reach 100%.

As expected from this data, the *P. lobata* stands vary also in their vegetation: 46 of the 97 vascular plant species recorded were found only once in the 19 stands shown in the Appendix 1. Of these species, 22 are neophytes in Switzerland (according to Moser *et al.*, 2002). This is not surprising, since the sites with *P. lobata* are vulnerable also regarding the invasion by other neophytes, particularly because most of these originate from (sub)tropical climate, as is the case for *P. lobata.*

Growth rate and spread

The rapid growth of *P. lobata* starts in the seedling stage. Pron (2006) found that 5–7 days old seedlings transplanted into fertile garden soil developed a main root of up to 30 cm and two to three shoots of up to 1 m length within 3 months. In the study region, it was also observed that, after all aerial parts of *P. lobata* had been cut above a well-rooted node in spring, new runners of up to 2 m in length developed in all directions within 3 months (Pron, 2006; fig 17). Mitich (2000) reported that as many as 30 vines can rapidly radiate from a single root crown. The maximum shoot growth of 26 cm per day observed in Southern Switzerland is slightly less than the 30 cm per day reported by Blaustein (2001) for the South-Eastern USA.

A simple model can describe the enormous increase of an area covered by *P. lobata* taking place in the course of only a few years. As a starting point for the model it is practical to take a circular, well-established *P. lobata* stand with a radius of 2 m, i.e. an area of 12.56 m^2. If the surrounding site is favourable, the stand will expand approximately 10 m per year radially in all directions. After n years the radius R_n of the stand will be: $R_n = 2\text{ m} + n \times 10\text{ m}$

The surface area A_n after n years will be $A_n = (2\text{ m} + n \times 10\text{ m})^2 \times \pi$

Thus, after 1 year, the surface area covered by *P. lobata* will increase by 615 m^2, after 2 years by in total 3629 m^2, and after 5 years by 9156 m^2. This enormous growth makes in understandable that, in the South-Eastern USA, in the last 70 years (Mitich, 2000), the area covered by *P. lobata*, planted at hundreds of sites, grew to 3 million hectares of so-called Kudzuland (Forseth & Innis, 2004). In Switzerland, Pron (pers. comm.) reported that near Ascona (site 2 in the Appendix 1) 3 m long shoots of *P. lobata* had to be cut back three times every year to prevent a road being overgrown. Near Caslano (site 5 in the Appendix 1), in the last few years, the 2000 m^2 *P. lobata* stand was annually cut back to the soil surface but regularly recovered completely within 1 year.

Several factors contribute to this enormous growth: (i) *P. lobata* can improve the nutrient status of the soil, particularly because it fixes atmospheric nitrogen in its root nodules (Shurtleff & Aoyagi, 1977); (ii) the roots that develop at the nodes every 0.3–0.6 m along the shoot (Mitich, 2000) supply additional water and nutrients to the plant; (iii) relatively little biomass is allocated to structural support, allowing a larger investment in shoot growth and photosynthetic tissue (GISD (Global Invasive Species Database), 2010); (iv) *P. lobata* overgrows the other vegetation and thus has optimal light conditions, also by rapidly orienting its leaflets in relation to the sun (Forseth & Teramura, 1986); (v) no significant leaf damage was observed in Southern Switzerland. This is in contrast to the impact of the 116 species of phytophagous insects and of the foliar pathogens found by Sun *et al.* (2006) on *P. lobata* in its native habitat in China.

Effects on biodiversity

A species with this high a growth rate threatens local biodiversity (Mitich, 2000; Blaustein, 2001; Forseth & Innis, 2004). In unmanaged *P. lobata* plots in Southern Switzerland, it was found that the number of plant species is approximately half that of neighbouring environmentally similar forest plots (on average 11 vs. 20 species, Table 1). As already mentioned, among the species affected by *P. lobata* one is classified as vulnerable and two are classified as near threatened in the Red List. Furthermore, the cover and vitality of the plant species in the unmanaged *P. lobata* plots were often very low. A reason for this is certainly the shade cast by the up to 2 m thick mats of shoots and litter of *P. lobata*. Root competition may also play a role.

Forseth & Innis (2004) state that the negative effects of *P. lobata* on many plant species affect the animals associated with them. In a pilot study at the sites at Magliaso and Caslano, Pron (2006) found that between April 24 and July 5, 2006, the number of taxa and individuals of soil surface arthropods under dense *P. lobata* stands was clearly smaller than in neighbouring environmentally similar forests without this species.

Genetics

Genetic investigations (AFLP analysis) by R. Kölliker (Agroscope Zurich, pers. comm.) provide an insight into the origin of the *P. lobata* plants established in Southern Switzerland. Sixteen accessions from this region and six from the USA had a very low genetic variability and a lack of a clear grouping, indicating that they all originated vegetatively from related source plants. (Additional data of Kölliker showed large genetic differences between the Swiss and

American accessions compared to those from China and Thailand; Heider *et al.* (2007) documented a large polymorphism among the populations of China). A further indication that the *P. lobata* stands originated mostly from vegetative propagation is that none was at a distance of more than 20 m from gardens. If propagation by seed had occurred, stands at greater distances from gardens should have been found. This pattern is in agreement with the poor seed dispersal and seedling establishment reported for the USA by Forseth & Innis (2004), and with the poor seed germination rate of only 20% (after 73 days) of unscarified seeds found in the study region by Pron (2006). (Mechanically scarified seed had a germination rate of 100%). Similar results were obtained by Duke (1983) and by Susko *et al.* (1999). Further studies would be needed to determine whether germination is promoted by the passage through the gut of particular animal species.

Conclusions

Comparison between the situation in Switzerland and the USA

The data presented in this paper show that the ecology of *P. lobata* in Southern Switzerland is similar to that in the South-Eastern USA described by Duke (1983), Miller & Edwards (1983), Susko *et al.* (1999), Mitich (2000), Blaustein (2001), Forseth & Innis (2004), Jarnevich & Stohlgren (2009) and Coiner (2012). This concerns the types of habitats and soils where the species occurs, and its growth and establishment pattern. As mentioned, the data of Kölliker (pers. comm.) demonstrate that even the genetics of *P. lobata* from the USA and Switzerland are very similar.

In the USA, during the first half of the 20th century, over 85 million seedlings of *P. lobata* were provided to landowners by government agencies for use as a forage crop and for erosion control, which then led to the invasion of 3 million hectares, causing immense damage to biodiversity, agriculture, forestry and infrastructure (Miller & Edwards, 1983; Mitich, 2000; Blaustein, 2001; and Forseth & Innis, 2004). Introduction of *P. lobata* at such a scale has never taken place in Switzerland and the damage caused until now is minor (see also Pron, 2006).

Climatic considerations

To investigate what could happen to the existing *P. lobata* stands in Switzerland the potential distribution of this species in relation to the climate (and climate change) in Switzerland was compared with the distribution of this species in relation to the climate in the Eastern USA. Detailed climatological and physiological investigations by Coiner (2012) show that, in regions with moist temperate climate, the occurrence of *P. lobata* is not limited by cold winter temperature, as was assumed by Shurtleff & Aoyagi (1977), Miller & Edwards (1983) and EPPO (2007). Coiner (2012) states that, in the Eastern USA, *P. lobata* "has migrated northward in concert with the northward shift in the −20°C minimum winter temperature isocline". This explains why stands of the species are found in New Jersey, New York City and Connecticut (Mitich, 2000), and even in southern Ontario (Coiner, 2012). Large parts of lowland Switzerland, i.e. below 700 m, have a moist temperate climate with mean monthly temperatures for the coldest month, i.e. January, that are higher than −10°C (data for 1981–2010, Meteoschweiz, 2014). Thus, *P. lobata* can persist in these regions. This was the case in Zurich, i.e. North of the Alps, where individuals grew very well in two gardens for at least 20 years until they were eradicated in 2012 (Pron, 2006; P. Enz and P. Meyer, Zurich, pers. comm.). *P. lobata* also grows in the open at several locations in Germany, e.g. in the Botanical Garden of Halle (Biologie.uni-halle, 2014). However, it cannot be excluded that *P. lobata* cultivars or clones with different climate requirements grow at these different localities. All this data suggest that *P. lobata* can persist not only in the (sub)mediterranean region but also in large parts of Central Europe that have mild winter climate, i.e. in the regions with so-called grape climate, e.g. in the Rhine valley just North of Basel.

In Southern Switzerland, the region climatically suitable for *P. lobata*, i.e. situated at approximately <700 m altitude, comprises 591 km^2 (calculation and pers. comm. by D. Trüssel, Zurich). In fact, *P. lobata* occurs not only, as already described, in the immediate vicinity of the lakes Lugano and Maggiore, but also at two sites situated at more than 200 m above Lake Maggiore, and at three sites at 10–20 km from this lake (Mt. Trinità and Orselina, respectively at Pollegio, S. Vittore and at Osogna at 770 m; see data at www.infoflora.ch). But why are 27 of the 32 stands of established *P. lobata* described at www.infoflora.ch situated at a horizontal distance of less than only 400 m and at a vertical distance of less than only 200 m from the Lakes Lugano and Maggiore? The reason for this may be the gardening tradition in Southern Switzerland.

History of *P. lobata* in Switzerland

Already from the 1880s onwards it was fashionable to cultivate exotic species such as *P. lobata* in parks and gardens near these lakes, as is documented by the species lists of Schröter (1956). Thus, *P. lobata* does not occur in other regions of Southern Switzerland because it was not planted in these regions, and because it very probably fails to disperse with seeds (Meisenburg & Fox, 2002) and has a low germination rate (see above). Furthermore, the spread of *P. lobata* is restricted because the great majority of the stands are at <20 m from settlements and are therefore mostly controlled. In fact, 15 of the 16 stands for which information is available are mown or treated with herbicides (Appendix 1).

Future projections

Possible effects of climate change on the distribution and environmental threat of *P. lobata* in South-Central Europe have been modelled by Follak (2011). He predicts that several regions of Austria, Slovenia, Northern Italy and even the Rhine valley between Germany and France will become at least marginally suitable for *P. lobata*. Surprisingly, Follak (2011, fig. 3) does not classify Southern Switzerland as suitable for this species, however he notes that the climate grid he used may not be representative for this region because of its sharp topographic gradients and because of the influences of the Lakes Lugano and Maggiore. As described above *P. lobata* also grows where there are no climatic effects from these lakes.

Walther (2002) and Walther *et al.* (2007) documented that near Lake Maggiore, the value and frequency of the minimum temperature as well as the length of the growing season (9 months in the 1950s and 10.5 months in 2005–2006) have shifted towards warmer conditions. One can assume that this may lead to an enhanced spread, possibly also because of a better seed germination and establishment, and thus to a more difficult control of the (sub)tropical species *P. lobata*. Such a spread could be similar to the enhanced generative spread taking place in Southern Switzerland of the neophytic species *Prunus laurocerasus* and *P. serotina,* as well as *Lonicera japonica* (Zäch *et al.*, 2006; and pers. observations by A. G.). An increased growth of *P. lobata* may also be expected in response to an increased concentration of atmospheric CO_2, as can be deduced from the data of Sasek & Strain (1989) and Forseth & Innis (2004). An enhanced spread and growth of *P. lobata* might more strongly affect biodiversity and lead to problems in agriculture, forestry and infrastructure. In order to prepare against such problems, methods for the control of the species have been developed in Southern Switzerland by Buholzer *et al.* (accepted), as recommended by EPPO.

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Écologie et répartition de la liane invasive du sud-est de l'Asie Kudzu, *Pueraria lobata* (Fabaceae) en Suisse méridionale

Pueraria lobata, ou Kudzu, est une liane pérenne originaire des régions tempérées à tropicales de l'est de l'Asie. Introduite comme plante ornementale dans de nombreuses régions (sub)tropicales et comme plante fourragère dans le sud-est des États-Unis, elle s'est propagée végétativement dans les forêts et prairies adjacentes, et a aussi été dispersée via des déchets de jardin. Les objectifs de notre article sont: (i) de déterminer si l'écologie de *P. lobata* en Suisse méridionale est semblable à celle au sud-est des États-Unis, où elle cause des dégâts importants; (ii) de faire des pronostics quant à sa possible dissémination en Suisse méridionale, où il y a déjà 32 peuplements couvrant 16 200 m2. Les tiges croissent ≤26 cm/jour et ≤11 m/an, formant des tapis d'une épaisseur ≤2 m. Dans les peuplements de *P. lobata* le nombre d'espèces de plantes par site est environ deux fois plus faible que celui de sites semblables sans cette espèce. Nos résultats montrent que l'écologie de *P. lobata* en Suisse méridionale est semblable à celle décrite aux États-Unis. Les exigences climatiques de *P. lobata* sont tellement larges qu'elle pourrait s'établir dans de nombreuses régions d'Europe méridionale et centrale. Cependant, elle ne se disséminera vraisemblablement pas à grande échelle en Suisse, d'une part parce que la germination de graines est limitée, d'autre part parce que ses peuplements sont proches de zones habitées et de ce fait contrôlés

Экология и распространенность в южной части Швейцарии инвазивной лианы кудзу, *Pueraria lobata* (Fabaceae), произрастающей в Юго-Восточной Азии

Pueraria lobata, кудзу, является многолетней лианой, естественно произрастающей в районе от умеренной до тропической зоны Восточной Азии. Завезенная главным образом как декоративное растение во многие (суб) тропические районы, а также как фуражная сельскохозяйственная культура в юго-восточные области США, это растение распространилось на близлежащие леса и поля и было также рассеяно вместе с садоводческими отходами. Цели настоящей статьи: (i) оценить, в какой степени экология *P. lobata* в южной Швейцарии аналогична его экологии на юго-востоке США, где это растение наносит большой ущерб; (ii) спрогнозировать его дальнейшее распространение в южной части Швейцарии. В этой стране он встречается уже в 32 местах и охватывает 16 200 кв.м; побеги прирастают до 26 см в сутки и до 11 м в год, образуя покров, доходящий до толщины в 2 метра. На площадях, занятых *P. lobata,* наблюдается примерно в два раза меньше видов растений по сравнению с аналогичными площадями без него. Статья показывает, что экология *P. lobata* в южной части Швейцарии аналогична описанной для США. Широкий размах климатических требований этого вида позволяет предположить, что он способен акклиматизироваться во многих областях Южной и Центральной Европы. Однако не предполагается, что это растение широко распространится в Швейцарии, так как не была отмечена его акклиматизация из семян, а также еще и потому, что его образования всегда наблюдаются в

непосредственной близости от поселений и, таким образом, могут в большой степени подвергаться борьбе.

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Appendix 1

The vegetation table which follows shows relevés (surveys) of 19 *Pueraria lobata* stands and their accompanying species (with cover/abundance values after Braun-Blanquet, see methods) in Southern Switzerland. The species are ordered by frequency. Abbreviations for the management (often only at the margin of the stand): m = mowing at least once a year; c = sporadic application of chemicals; 0 = no management. N = neophyte, according to Moser *et al.* (2002); P = protected in Switzerland, according to Lauber *et al.* (2012). Further species. Relevé number: Braun-Blanquet value: N. *Artemisia verlotiorum* 2:3; 3: (1); *Taraxacum officinale* aggr. 2:+, 17:+; *Dryopterix filix-mas* 3:1, 15:1; *Medicago lupulina* 5:+, 6:r; *Chenopodium album* 2:1, 5:+; N. *Cinnamomum glanduliferum* 3:1, 11:(r); N. *Galinsoga ciliata* 16:1, 17:1; *Galium aparine* 8:2; 10:(1); *Prunus avium* 2:1, 14:1; *Tamus communis* 7:+, 10:1; *Tilia cordata* 1:(+), 2:1; *Fragaria vesca* 3:+, 7:1; *Galium mollugo aggr*. 16:+, 17:+; *Molinia arundinacea* 16:1, 17:1; *Polygonum multiflorum* 3:1, 10:1; N. *Rhododendron* sp. 18: (+), 19:(+); *Sonchus asper* 5:+, 17:+; *Trifolium campestre* 1:+, 18:+; *Alnus glutinosa* 2:1, *Trifolium pratense* 6:+; *Acer campestre* 9:1; *Acer pseudoplatanus* 13:+; *Equisetum arvense*. 6:+; *Hordeum murinum* 6:r; *Humulus lupulus* 17:r; *Parietaria judaica* 18:1; *Plantago lanceolata* 6:+; *Populus alba* 18:r; *Rumex scutatus* 2:1; *Vicia cracca* 10:(1); *Anagallis arvensis* 5:1; *Anthoxanthum odoratum* 3:1; *Betula pendula* 14:1; *Brachypodium pinnatum* 5:+: *Bromus sterilis* 1 (+); *Capsella bursa-pastoris* 2:+; *Carpinus betulus* 19:1; *Celtis australis* 7:+; *Chaenorrhinum minus* 5:+; P. *Cistus salviifolius* 13:(+); N. *Conyza canadensis* 16:1; *Crepis taraxacifolia* 1:+; N. *Elaeagnus pungens* 7:r; *Euphorbia peplus* 5:1; *Ficus carica* 7:r; *Helianthemum nummularium* s.l. 5:+; *Hieracium murorum* s.l. 1:1; *Holcus lanatus* 1:+; *Hypericum perforatum* 10:(1); *Ilex aquifolium* 15:+; *Lactuca serriola* 18:+; *Lamium montanum* 1:+; N. *Ligustrum lucidum* 11:(r); *Lysimachia vulgaris* 3:+; *Ornithogalum pyrenaicum* 10:+; *Poa pratensis* 8:1; *Quercus rubra* 3:(1); *Ranunculus acris* s.l. 8:+; *Setaria viridis* 5:3; *Silene vulgaris* 2:1; *Taxus baccata* 3:2; *Thlaspi arvense* 5:+; *Verbena officinalis* 5:1; N. *Veronica persica* 5:2; *Vicia tetrasperma* 10:(1).

Site number	1	2	3	4	5	6	7	8	9	10
Location	Cassina d'Agno	Ascona	Ascona	Ascona	Caslano	Caslano	Caslano	Croglio	Locarno	Magliaso
Coordinates	45°59′39.1″ 8°53′34.8″	46°09′11.5″ 8°44′50.8″	46°09′27.6″ 8°45′45.3″	46°09′25.3″ 8°45′54.1″	45°57′33.2″ 8°52′34.8″	45°57′33.4″ 8°52′43.4″	45°57′34.0″ 8°52′37.4″	45°58′19.0″ 8°51′11.4″	46°10′22.7″ 8°46′58.25″	45°59′17.4″ 8°53′32.6″
Altitude [m]	340	330	300	295	275	272	278	280	400	290
Exposure	ESE	SSE	SSE	SSE	S	S	S	SW	S	SE
Slope [°]	30	30	10	10	20	50	20	20	30	40
Stand size m^2	1500	570	180	30	2000	60	50	1750	500	6500
Relevé area m^2	200	200	180	30	200	60	50	200	200	200
Management	m+c	0 + m	m	m	c	m	m	m	m?	m
Date of the relevé	30. 06. 06	07. 06. 06	07. 06. 06	07. 06. 06	06. 06. 06	30. 06. 06	30. 06. 06	06. 06. 06	08. 06. 06	30. 05. 06
N.Pueraria lobata	4	4	2	4	5	2	2	4	4	5
Rubus fruticosus s.l.	+	1	1	.	2	+	1	1	.	1
N. Lonicera japonica	+	–	1	.	+	+	1	1	.	.
Calystegia sepium	1	1	1	.	+	1	.	1	.	1
N. Robinia pseudoacacia	(1)	+	–	–	–	–	–	(1)	(1)	(1)
Castanea sativa	(+)	2	(1)	–	–	–	–	(2)	–	–
Hedera helix	1	1	+	–	–	(r)	1	+	–	–
Sambucus nigra	(+)	–	2	+	–	–	–	r	(1)	1
Fraxinus excelsior	–	1	–	–	–	–	–	–	–	+
N.Trachycarpus fortunei	–	1	3	–	–	–	3	–	1	–
N. Ailanthus altissima	–	r	–	–	1	1	3	–	–	–
N. Erigeron annuus s.l.	r	–	+	–	+	–	–	1	–	–
N. Phytolacca americana	–	–	–	r	–	–	–	1	1	+
N. Prunus laurocerasus	–	–	2	(2)	–	–	–	–	1	–
Urtica dioica	+	2	–	–	–	–	1	1	–	–
Crepis biennis	2	–	–	–	+	+	–	–	–	–
Quercus petraea	–	–	–	–	–	–	–	(2)	–	–
Carex spp.	–	–	1	2	–	2	2	–	–	–
Clematis vitalba	–	–	–	–	+	–	–	–	1	–
Corylus avellana	–	1	–	–	–	–	–	–	–	–
Impatiens parviflora	–	–	1	–	–	–	–	2	–	–
N. Parthenocissus quinquefolia	–	–	–	–	–	–	–	–	–	(1)
Chelidonium majus	+	1	–	–	–	–	–	1	–	(1)
Athyrium filix-femina	–	–	–	–	–	–	–	4	–	–
Oxalis acetosella	+	–	–	–	r	–	–	+	–	–
N. Phyllostachys sp.	–	2	–	–	–	–	(2)	–	–	–
Rumex obtusifolius	+	–	–	–	–	(r)	–	–	–	–
N. Buddleja davidii	–	–	–	–	+	–	–	–	–	–
Euonymus euroaeus	–	–	–	–	–	–	1	+	–	1
Plantago major	(+)	–	–	1	–	+	–	–	–	–
N. Reynoutria japonica	–	–	–	–	3	–	–	–	3	–
Tilia platyphyllos	–	–	–	–	–	–	–	–	(1)	–
Verbascum densiflorum	–	–	–	–	1	+	–	–	–	(+)
Species/relevé	22	22	21	6	24	16	15	20	10	18
Site number	1	2	3	4	5	6	7	8	9	10

11	12	13	14	15	16	17	18	19	
Porto Ronco 46°08′54.0″ 8°44′07.1″″ 215 SSE 80 100 100 m 08. 06. 06	Porto Ronco 46°08′49.0″ 8°43′58.6″ 215 SE 80 80 80 m 08. 06. 06	Ronco s. Ascona 46°09′09.2″ 8°44′42.8′ 360 SE 20 400 200 ? 07. 06. 06	Ronco s. Ascona 46°09′10.4″ 8°44′45.2′ 350 SSE 10 300 200 ? 07. 06. 06	Ronco s. Ascona 46°09′10.2″ 8°44′41.9″ 360 NE 30 100 100 ? 07. 06. 06	Sant' Abbondio 46°06′16.0″ 8°45′32.5′ 220 NW 45 300 200 m 01. 08. 06	Sant' Abbondio 46°06′20.7″ 8°45′39.8 210 NW 30 50 50 m 01. 08. 06	Vico Morcote 45°55′36.0″ 8°55′17.6 295 SE 60 500 200 m 08. 08. 06	Vico Morcote 45°55′39.0″ 8°55′22.4″ 285 SE 45 80 80 0 31. 07. 06	Frequency
3	3	3	3	2	5	5	5	5	19
.	1	.	2	.	.	1	1	1	13
.	2	+	1hh	2	.	.	.	1	12
.	.	.	+	.	1	+	1	.	11
–	–	+	–	–	–	2	(2)	1	9
(2)	–	+	2	2	–	1	–	–	9
–	–	+	–	–	–	–	+	–	8
–	1	–	–	–	–	2	–	–	7
–	1	+	1	2	–	1	–	–	7
–	–	–	–	–	(r)	–	–	–	5
–	–	+	–	–	–	–	+	–	5
–	–	–	–	–	+	–	–	–	5
–	–	–	–	–	(+)	–	+	–	5
–	–	+	–	–	–	–	–	(3)	5
–	–	–	–	–	–	1	–	–	5
–	–	–	–	–	+	+	–	–	5
+	1	+	1	–	–	–	–	–	5
–	–	–	–	–	–	–	–	–	4
–	–	+	–	+	–	–	1	–	4
–	–	–	–	1	r	(1)	–	–	4
–	–	–	2	–	+	–	–	–	4
–	–	+	–	–	–	–	1	2	4
–	–	–	–	–	–	–	–	–	4
–	–	+	1	–	+	–	–	–	4
–	–	–	–	–	r	–	–	–	4
–	–	(1)	–	–	–	–	–	–	3
–	–	–	–	–	–	+	–	–	3
–	2	–	–	–	–	–	(+)	–	3
–	–	–	–	–	–	–	–	–	3
–	–	–	–	–	–	–	–	–	3
–	–	–	–	–	–	+	–	–	3
–	1	–	–	–	–	–	–	2	3
–	–	–	–	–	–	–	–	–	3
5	8	15	11	8	14	18	15	9	
11	12	13	14	15	16	17	18	19	