Environmental Barriers to Hybridization between Iris tenax Dougl. and Iris chrysophylla Howell[1]

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THE SPECIES discussed in this report are closely related members of the series *Californicae.* They are native plants of the area west of the crest of the Cascade Mountains of Oregon and Washington, with *Iris chrysophylla* probably extending some distance into California. *I. tenax* is essentially a species of the interior valleys, although it does extend into the coast mountains and along a narrow maritime strip. It is not found in forested areas except where the forest has been removed by logging, highway construction, or some natural phenomenon. *I. chrysophylla* is abundant in southwest Oregon and in a number of locations in the northern Cascade Mountains at moderate elevations. Two small, localized populations are known from the coast range of Oregon (Clarkson, 1955). In the coast and Cascade mountains it is a species inhabiting rocky, well-drained soils with little herbaceous competition.

Morphologically, the two are typical Irises differing from each other in a quantitative manner only. They are readily distinguished by any of the following traits but indistinguishable by other floral or vegetative characteristics: *I. tenax*—perianth tube 5-10 mm. long; bracts alternate and linear; flowers purple to white, occasionally yellow. *I. chrysophylla*—perianth tube 4-10 cm. long; bracts opposite and lanceolate; flowers pale yellow. They are uniform in chromosome morphology and number (2N=40) and produce highly fertile hybrids when crossed (Smith and Clarkson, 1956).

Natural hybrids have been found at three locations in Oregon (Clarkson, 1955). Each site is at the border of the natural range of *I. chrysophylla* under disturbed conditions which have allowed *I. tenax* to invade an area it has previously not occupied. True intermediate forms are rare, but there is abundant evidence of introgression of *I. chrysophylla* traits into *I. tenax.* The reverse of this introgression apparently does not occur.

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[1]The author regards the taxa concerned in this report to be of subspecific status. However, until valid publication is completed, they must be treated in accord with nomenclatural rules. The research upon which this report is based was financed by National Science Foundation grant NSF-G-3417.

Because the only barriers to hybridization seem to be ecological, this study was initiated to investigate the role of the environment in the isolation of these taxa and to determine how habitat disturbance alters the environment to make hybridization possible. These factors were analyzed: (1) the ecological requirements controlling the distribution of *I. chrysophylla;* (2) the ecological requirements controlling the distribution of *I. tenax;* (3) how a disturbed habitat provides a suitable environment for *I. tenax* but not *I. chrysophylla.*

Procedure

Because of the apparent uniformity of habitats, detailed work was limited to two areas of hybridization with only cursory examination of the other. Five randomly distributed circular plots of one-meter radius were established in each of the sites discussed below. Cover and frequency of species were recorded for all plots at least twice during the year. Sites 1-7 were checked every two weeks from May to mid-August and were further examined for other data as detailed in a following section.

1. Peavine ridge, 12 miles southwest of McMinnville, Oregon, in the foothills of the coast range. This area was logged 20-30 years previously and contains an excellent colony of *I. tenax.* The site selected is a gentle, south slope separated by a gravel road from an unlogged area where *I. tenax* does not grow.

1a. The unlogged area mentioned above was studied to determine the nature of undisturbed habitats.

2. Along Mill Creek, about six miles west of Dallas, Oregon. This is one of the two known locations of *I. chrysophylla* in the coast range and one of three areas of hybridization.

3. Two miles east of Mehama Junction along Oregon state highway No. 22. This is a good roadside colony of *I. tenax* in cut-over land originally consisting of Douglas fir with a scattering of oak (*Quercus garryana*).

4. A south slope ¼ mile west of the Detroit dam, North Santiam River. This is a colony of *I. tenax* characterized by a predominance of white and pale-blue flowered forms indicating hybrid origin. Directly across a steep canyon to the east is a colony of *I. chrysophylla.*

5. The *I. chrysophylla* colony mentioned above. This stand is on a west-facing slope.

6. An *I. chrysophylla* colony one mile east of the town of Detroit.

Along state highway No. 22. This site is of particular interest because in an adjacent grass-covered section Irises are not found. The area has been logged and burned and is, therefore, somewhat atypical.

6a. An area adjacent to the one above but heavily forested by Douglas fir and with complete ground cover provided by *Berberis nervosa* (Oregon Grape) and *Gaultheria shallon* (Salal). *I. chrysophylla* does not grow in this area, and the site was studied only for comparison purposes.

7. An *I. chrysophylla* colony, ½ mile west of the North Santiam River and about 10 miles east of Marion Forks, Oregon. Along state highway No. 22.

8. Roadside, west city limits of Gates, Oregon, along Oregon state highway No. 22. Originally a Douglas fir forest in the valley of the North Santiam River. This site is now a mixture of roadside weeds and *I. tenax.*

9. Roadside colony of *I. tenax* 20 miles west of Portland, Oregon, along Scholl's road.

10. An *I. tenax* colony in an orchard, six miles northwest of McMinnville, Oregon.

11. Along Scoggin's Creek, 10 miles southwest of Forest Grove, Oregon. This is a yellow-flowered colony of *I. tenax* sometimes referred to *I. tenax gormani* (Foster, 1937).

The first seven locations were selected to provide rough transects from typical *I. tenax* habitats through zones of hybridization and into typical *I. chrysophylla* habitats. The remaining sites were established to test variability of habitat type. In addition to study of the areas discussed above, an extensive reconnaissance was conducted over most of the range of both species as an additional test of the general validity of the data compiled.

Following evaluation of preliminary data, a number of transplants were made. These included: (1) transplants of *I. tenax* from Peavine Ridge (Site 1) to Site 6 (one mile east of Detroit) and of *I. chrysophylla* at Detroit (Site 6) to Peavine (Site 1); (2) transplants of *I. tenax* (Site 1) into the adjacent forested area at Peavine (Site 1a); (3) transplants of *I. chrysophylla* at Detroit (Site 6) into the adjacent heavily forested area (Site 6a). In addition to these field experiments, clones of *I. tenax* were grown under normal and reduced light conditions in the greenhouse. This experiment was conducted with the soil from Peavine Ridge in which *I. tenax* normally grows and with soil from the adjacent forested area where it does not grow.

Comparative Ecology of I. tenax and I. chrysophylla

Precipitation. Pertinent climatic data compiled from U.S. Weather Bureau reports are presented in Table 1. Long-term means are given because these probably provide better estimates of the effect of precipitation on distribution than do data for shorter periods. Data from three weather stations

TABLE 1. PRECIPITATION
Long-Term Means. 1932-1946 or at least 10 Years

	McMinnville	*Mehama*	*Detroit*
January	6.96	9.34	11.20
February	5.29	7.86	8.92
March	4.37	8.01	17.66
April	2.65	5.01	5.25
May	1.87	4.26	4.84
June	1.31	3.20	2.84
July	.38	.81	1.17
August	.48	1.64	.88
September	1.83	2.68	2.45
October	2.98	6.07	7.16
November	7.35	9.25	11.03
December	7.43	10.80	13.04

are given. These are near at least one of the sites studied in detail and provide a general picture of precipitation from the coast range well into the Cascade Mountains. Temperature data are not given because average monthly values are not of great significance as an indication of a limiting factor.

Associated species. Table 2 is a list of species found growing with the two *Iris* species. Not all species are found in all areas, but the general pattern is significant. It should be noted that these plants associated with *I. tenax* are mainly introduced species. These plants marked with an asterisk were found only at the *I. tenax* colony near the Detroit Dam (Site 4) which, as previously mentioned, is evidently of hybrid origin. No *I. tenax* plot had less than 40 per cent herbaceous cover (usually 80-90 per cent), and no *I. chrysophylla* plot had more than 20 per cent (usually 1-5 per cent). Shrub cover for *I. tenax* never exceeded 20 per cent while *I. chrysophylla* tolerated 40 per cent. Tree cover for *I. chrysophylla* ranged from 0 to 100 per cent while trees were not shading *I. tenax* plots. Other observations show that *I. tenax* is found under trees but not when the cover exceeds about 50 per cent. In summary, *I. tenax* tolerates a high degree of herbaceous competition but a minimum of tree and shrub competition. For *I. chrysophylla,* the situation is reversed.

TABLE 2. ASSOCIATED SPECIES. A COMPARISON OF I. CHRYSOPHYLLA AND I. TENAX

I. chrysophylla	*I. tenax*
Trees	
Tsuga heterophylla	None
Pseudotsuga menziesii	
Acer macrophyllum	
Cornus nuttallii	
Shrubs	
Vaccinium ovatum	Arctostaphylos columbiana*
Holodiscus discolor	Whipplea modesta*
Whipplea modesta	Berberis nervosa*
Acer circinatum	Rosa gymnocarpa*
Arctostaphylos columbiana	Rhus diversiloba
Berberis nervosa	Symphoricarpos albus
Gaultheria shallon	Corylus californica
Rosa gymnocarpa	Quercus garryana
Pinus contorta	Hypericum perforatum
Linnaea borealis	Gaultheria shallon*
Herbs Providing 10% or Greater Cover on Any Plot	
Carex sp..	Bromus carinatus
	Pteridium aquilinum pubescens
	Dactylis glomerata
	Lupinus polyphyllus
	Holcus lanatus
	Fragaria bracteata
	Lotus americanus
	Lotus micranthus
	Rubus vitifolius
	Trifolium pratense
	Equisetum arvense
Herbs and Small Shrubs Present but Providing Less than 10% Cover on Any Plot	
Rubus vitifolius	Cirsium lanceolatum
Pteridium aquilinum pubescens	Poa pratensis
Fragaria bracteata	Plantago lanceolata
Cirsium lanceolatum	Achillea millefolium
Trientalis latifolia	Prunella vulgaris
Epilobium minutum	Vicia americana
Rubus parviflorus	Rumex acetosella
Osmorhiza nuda	Sherardia arvensis
Trillium ovatum	Trientalis latifolia*

*Species marked with an asterisk are characteristically found associated with *I. chrysophylla.* At site No. 4 near the Detroit Dam they are found with an *I. tenax* colony of hybrid origin.

Light. A light meter was used to ascertain the amount of light actually reaching individual *Iris* plants. Data were recorded for a variety of conditions ranging from full sunlight to dense cloudiness. Thirty measurements in each of the areas show that *I. tenax* does not grow where light is reduced to less than 11 per cent of that available in the open. *I. chrysophylla* tolerates habitats in which the light is reduced to only 2 per cent of that available in the open. Further corroboration of the light requirements of *I. tenax* is provided by the fact that the species is no longer present in a site near the Detroit Dam where it was collected in abundance in 1955. The only change in the habitat since that time is a dense growth of Bracken fern (*Pteridium aquilinum pubescens*) which has reduced the light at surface level to less than 5 per cent throughout. Moisture or nutrient competition, in this case, may be an additional factor, but the ability of *I. tenax* to compete with herbaceous cover at other sites makes this doubtful.

As a further test of the effect of the light factor, *I. tenax* at Peavine was transplanted into the adjacent forested area. Of 12 plants tested, none produced more than a few shoots of two-three-inch length although the soil remained moist. The effect of transplanting was checked by transplanting within the *I. tenax* habitat and to a home plot. No losses occurred. Clones of *I. tenax* were also transplanted to the greenhouse. After becoming established, one member of each of four pairs was grown in normal light and the other in light reduced to 10 per cent of that available. All those grown in normal light were growing vigorously after four months, while those in the shade died in three weeks. To eliminate soil as a factor, the experiment was repeated with soil from the forested area. A similar response was noted. Further experiments were conducted with seedlings with the same reaction except that the seedlings do not survive as long under shaded conditions. This is presumably due to a smaller reserve food supply.

A few *I. tenax* plants were noted at the edge of wooded areas. These are characteristically etiolated, and none were seen producing flowers.

Soil. Textural differences between soils on the *I. tenax* sites and the *I. chrysophylla* sites are striking. Three samples from each site were screened with a two-millimeter mesh. Gravel and large rock make up from 10 to 30 per cent of the total soil volume on *I. tenax* sites, with the exception of the area near the Detroit Dam (Site 4). The remaining material is composed largely of fine particles and classified, hydrometrically, as silt loam. *I. chrysophylla* soils are more variable than *I. tenax* soils but are composed of a greater percentage of rock and gravel. The percentage of rock and gravel particles on *I. chrysophylla* sites ranges from 20 to 90 per cent of the total soil mass.

However, only one site had a gravel percentage less than 50 per cent, and two of the four areas sampled had soils composed of from 80 to 90 per cent gravel and rock. The soil at the *I. tenax* site (Site 4) near Detroit Dam is indistinguishable from *I. chrysophylla* soils, being composed of 85 per cent gravel and rock.

Soil pH throughout all the areas sampled ranged from 4.5 to 5.5 with no apparent distinction between species. Tests of phosphorus and nitrogen content show no species correlation for the former but a somewhat lower percentage of total nitrogen in *I. chrysophylla* sites. Four different tenax sites tested gave a range from .21 to .34 per cent total nitrogen. Of three chrysophylla sites only one tested over .17 per cent, and this (Site 6 with .34 per cent) had been burned over. The tests were conducted with screened soil so that actual nitrogen content per total soil volume is actually lower than reflected in soils tests and the difference between species much greater than indicated because of the greater rock content of *I. chrysophylla* soils. The low incidence of herbaceous species on *I. chrysophylla* sites is probably a reflection of nitrogen concentration.

Soil-moisture measurements were conducted with fibreglass blocks and measured with a Coleman meter. Blocks were placed at nine- and 14-inch depths on all plots of the seven habitats studied in detail. Permanent wilting percentage determinations were made by standard phytometric procedures for three *I. tenax* sites and three *I. chrysophylla* sites. Results reflect the greater variability of chrysophylla soil texture and also reflect the high percentage of fine soil particles of *I. tenax* soils. For *I. chrysophylla* soils the figures are: 4.4, 8.7, and 11.0 per cent. For *I. tenax* soils they are: 12.4, 16.1, and 14.2 per cent. Fibreglass blocks were placed in the containers and resistances recorded at the permanent wilting point. Field soil moisture as measured with fibreglass blocks indicates that the permanent wilting point was not reached at either the nine- or 14-inch depth at any time during the year as measured over a two-year period. Although direct comparison of laboratory and field resistance readings is invalid because of soil disturbance in the former, a broad relationship can be expected. Also, Table 1 shows that rainfall averages quite high through June at all sites.

Phenology. Both species normally begin growth in late March or early April and flower beginning about late April. Fluctuations due to elevation and seasonal variation occur but affect both species. No apparent phenological differences between the two species have been detected. Reciprocal transplants indicate that the transplanted species begins growth and (if flowering occurs) flowers at the same time as the nontransplanted taxon.

Transplanting. Much of the information gained from transplanting has already been presented under other headings. However, the response of the two species under reciprocal transplants is noteworthy. *I. tenax* in an *I. chrysophylla* site grows well and flowers, but of 10 individuals transplanted, none survived the first season of growth. *I. chrysophylla* transplanted to an *I. tenax* site at Peavine initiated leaves but did not flower and did not survive the first summer. Of equal interest, *I. tenax* plants from Site 4 transplanted to Peavine behaved as the *I. chrysophylla* plants. This is another indication of their hybrid origin. Although morphologically most like *I. tenax,* they are ecologically more closely related to *I. chrysophylla.* When transplanted to neutral, fertile conditions, both species thrive (Smith and Clarkson, 1956).

Summary. Table 3 presents a summary of the pertinent ecological characteristics of the two species.

TABLE 3. SUMMARY OF ECOLOGICAL CHARACTERISTICS

	I. chrysophylla	*I. tenax*
Associated species	Native species predominately trees and shrubs	Introduced species predominately herbaceous
Cover		
Herbs	20 per cent or less	40 per cent or greater
Shrubs	To 40 per cent	20 per cent or less
Trees	0-100 per cent	None
Light	2-100 per cent of available light	Not less than 11 per cent of available light
Soil		
Texture	20-90 per cent rock (Usually over 50 per cent with 80-90 per cent most common) Remainder loamy sand	10-30 per cent rock Remainder silt loam
pH	4.5-5.5	4.5-5.5
Permanent Wilting Percentage	4.4, 8.7, 11.0	12.4, 16.1, 14.2
Soil Moisture (Field)	Not below PWP at 9 or 14 inches	Not below PWP at 9 or 14 inches
Fertility	Nitrogen deficient	Moderately fertile

Conclusions

From the areas studied in some detail and from additional observations throughout the range of both species, three conclusions can be drawn:

1. *I. tenax* is limited in its distribution primarily by light. Disturbance of the habitat by logging or other factors tends to open the site so that light is increased and *I. tenax* becomes established. Observations of newly logged areas show that the species invades rapidly and flowers within two years after logging occurs. At Scoggin's Creek in Washington County, Oregon, the small population of *I. tenax gormani* seems to be diminishing due to an increase in shrub cover. Presumably the existence of *I. tenax* on any disturbed site is limited by the rate of secondary succession. Factors other than light, at least in northern Oregon, do not appear to be limiting, except for soil sterility which seems to prevent the species from invading *I. chrysophylla* areas.

2. *I. chrysophylla* appears to be limited by its inability to compete with grasses and other herbs. Therefore, disturbances which allow *I. tenax* to invade an area have no effect on *I. chrysophylla* unless the general level of soil fertility or moisture is so low as to prevent the establishment of herbaceous competition.

3. Man is the chief agent in the distribution of *I. tenax* because of his habitat disturbance. Therefore, most of the variability due to hybridization is probably quite recent in origin and difficult to assess in terms of species survival.

Literature Cited

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